Natural England Research Reports

Number XXX

Modelling study to determine the capacity of The Wash shellfish stocks to support eider *Somateria mollissima*

Richard Caldow, Richard Stillman and Andy West

CEH Dorset, Winfrith Technology Centre, Dorchester, Dorset. DT2 8ZD

ISSN 0967-876X

Cover note

Project officer	Conor Donnelly, Eastern Area Team, Conor.Donnelly@natural_england.org.uk
Contractor(s) (where appropriate)	Richard W G Caldow (rwgc@ceh.ac.uk) Richard A Stillman (rast@ceh.ac.uk) Andy D West (adwt@ceh.ac.uk) Centre for Ecology and Hydrology, CEH Dorset, Winfrith Technology Centre, Dorchester, Dorset. DT2 8ZD

This report should be cited as:
Caldow, R.W. G., Stillman, R. A. & West, A. D. 2007. **Modelling study to determine the capacity of The Wash shellfish stocks to support eider *Somateria mollissima.*** *English Nature Research Reports*, No XXX.

Acknowledgements

We gratefully acknowledge the provision of data concerning the results of shellfish stock surveys conducted in The Wash by Eastern Sea Fisheries Joint Committee (ESFJC) and the Centre for Environment, Fisheries and Aquaculture Science (CEFAS). We would also like to thank those officers of the ESFJC and CEFAS who attended project meetings and provided input to the project. In particular we would like to thank Matt Mander and Ron Jessop of ESFJC and Dave Palmer of CEFAS who provided valuable insights into and views on the shellfish stocks of The Wash throughout this project. We also acknowledge receipt of WeBS count data from the Wildfowl and wetlands Trust. Thanks are also due to Margaret Langran and Stephanie Smith of the CEH Library Service who collated most of the references listed in the bibliography.

Summary

This report presents the results of a research project carried out by the Centre for Ecology and Hydrology for Natural England in order to determine the capacity of The Wash shellfish stocks to support eider ducks *Somateria mollissima*.

Since 2003, mussel *Mytilus edulis* farmers on The Wash have reported high levels of mussel predation on their lays by eider ducks. In order to limit this predation some lay holders applied for consent from English Nature (now Natural England) to use scaring devices and some also applied to the Department of the Environment, Food and Rural Affairs (Defra) for a licence to shoot eiders. In advance of the public inquiry to address this conflict between eiders and the shellfish industry, Defra identified a need to develop knowledge and understanding of four key areas so that objective data would be available to facilitate decision making:

1. The eider population size in The Wash.
2. The number of eiders that the site can support when the mussel and cockle beds are in favourable condition.
3. The effectiveness of scaring devices in protecting the mussel stocks.
4. The impact of the scaring devices on eiders and non-target species.

This project was commissioned by Natural England to address the second key area. The principal aims of this project were as follows.

- To conduct a literature review of the current understating of eider feeding behaviour and scoping of modelling work.
- To develop and parameterise a model of eider ducks in The Wash.
- To validate this model against independent empirical data
- To conduct model simulations of a range of alternative shellfish stock/management scenarios in order to predict their effect on the level of eider duck mortality.

Over 100 published scientific papers and reports principally concerned with the ecology of diving dicks in general and eider in particular were collated and reviewed. The key points of relevance to the development of a behaviour-based model of the system were added to an existing Excel database arsing from a previous project on common scoters *Melanitta nigra*. This combined database is presented as a series of appendices to this report. This literature review provided information with which to parameterise the model and other independent data against which to validate it.

An existing behaviour-based model developed previously by CEH was parameterised to create a model of the populations of eider ducks and oystercatchers *Haematopus ostralegus* within The Wash and of the principle populations of shellfish that they exploit within it ie mussels, cockles *Cerastoderma edule* and American jack-knife clam *Ensis directus.* Parameterisation was based on information gleaned from the literature review and on the results of recent surveys of the shellfish stocks of The Wash conducted by Eastern Sea Fisheries Joint Committee, Centre for Environmental, Fisheries and Aquaculture Science and Ecomaris Ltd.

The output generated by the model was validated against independent data concerning: the proportion of time that birds spend feeding, their daily consumption of food, daily energy

expenditure, body mass, distribution and over-winter mortality. In all cases, the output of the model, when parameterised to mimic current day conditions in The Wash, fell within the likely range of expected values.

One series of model simulations was conducted to explore the consequences for the existing over-wintering populations of eiders and oystercatchers of changes to the total quantity of mussels available to them on the commercially cultivated lays against a number of alternative backgrounds in which the other shellfish stocks were varied in the light of the historical variation that they have shown. These simulations served to explore the impact on the existing eider and oystercatcher populations of a reduction in the stock of lay mussels and whether this impact varied in relation to the abundance of other shellfish stocks available to the birds.

A second series of model simulations was conducted to explore the consequences for the existing over-wintering populations of eiders and oystercatchers of changes to the distribution of the current total stock of mussels available to them on the commercially cultivated lays (c 10,000 tonnes) against a number of alternative backgrounds in which the other shellfish stocks were varied in the light of the historical variation that they have shown. These simulations served to explore the impact on the existing eider and oystercatcher populations of changes to the management of the commercially cultivated mussel lays and whether this impact varied in relation to the abundance of other shellfish stocks available to the birds.

In both of these series of simulations, the model was also used to predict the tonnage of shellfish removed by both eider ducks and oystercatchers from each of the shellfish stocks.

A third series of simulations was conducted in which the size of the peak population of eider ducks was varied and the stocks of the two 'un-natural' shellfish resources in The Wash ie commercially cultivated lay mussels and *Ensis directus* were set to either large or small values. These simulations were conducted to establish the extent to which the maximum size of the eider population that could be supported varied in response to variation in these two shellfish resources which appear to be currently of overwhelming importance to the eider population.

The key conclusions that can be drawn from all of these simulations are as follows:

1. The recent aggregation of eiders on the Roger and Toft lays can be explained purely in terms of the high density of high quality shellfish of a suitable size present there.

2. The proportion of the oystercatcher population that exploits the commercially cultivated mussel lays is far smaller than that of eiders.

3. Over-winter losses of mussels from lays to eiders and oystercatchers are estimated to be around 600 tonnes and 100 tonnes respectively. In the case of eiders this is entirely from the Roger and Toft lays.

4. The percentage of the peak eider population of 3,000 birds that cannot be supported under current circumstances is predicted to be around 4 per cent. This is in close agreement with independent estimates of the typical over winter mortality rate of eiders.

5. The percentage of the peak oystercatcher population of 15,000 birds that cannot be supported under current circumstances is predicted to be zero.

6. Provided that the stock of *Ensis directus* remains healthy, the stock of lay mussels could be reduced by up to 50 per cent without any significant effect upon the percentage of the eider population 'at risk'.

7. If the stock of lay mussels is reduced below around 50 per cent of its current value, the percentage of the eider population that could be supported is predicted to decline significantly, even in the presence of a healthy *Ensis* stock.

8. As the abundance of mussels on the best lays is reduced, eider predation on the remaining lays will increase and they will switch to alternative shellfish resources. This will not be sufficient to maintain the percentage of the population that can be supported at the current low value.

9. In the absence of a healthy stock of *Ensis*, the percentage of the eider population that can be supported is predicted to be far more vulnerable to any loss of access to lay mussel resources.

10. Variation in the abundance of cockles or mussels on the regulated beds was not predicted to significantly alter the effect on eider ducks of changes to the abundance of lay mussels.

11. Given most likely future shellfish stock scenarios, the population of oystercatchers, unlike that of eiders, is not predicted to be vulnerable to changes to the abundance of the lay mussel resource.

12. Increasing the extent to which the current stock of lay mussels is concentrated is predicted to increase the relative profitability of the already best areas to eider ducks and to result in increased losses from them and hence from lays as a whole (> 650 tonnes v c 600 tonnes currently).

13. Decreasing the extent to which the current stock of lay mussels is concentrated is predicted to decrease the relative profitability of the best areas to eiders, reduce predation pressure on the best lays and result in the losses of lay mussels decreasing (c 400 tonnes v c 600 tonnes).

14. Evening out variations in the numerical density of mussels between the lays is predicted to even out eider predation pressure between them.

15. Removing the best 'hot spots' of high mussel density on the lays is predicted to reduce the percentage of the eider population that can be supported.

16. The percentage of the oystercatcher population that is supported is predicted to be constant irrespective of changes to the way in which the lay mussel stock is distributed.

17. In contrast to eiders, increasing the extent to which the current stock of lay mussels is concentrated is predicted to reduce the profitability of the best lays to oystercatchers and to reduce losses from them. In contrast, spreading the mussels out more thinly increases the profitability of the best lays to oystercatchers and results in increased losses from them.

18. Because of the relatively minor predation pressure exerted on the lays by oystercatchers in comparison to eiders, changes to the overall losses from the lays mediated by changing the distribution of mussels are driven more by the responses of eider ducks than oystercatchers.

19. The current stocks of wild mussels on regulated beds and cockle stocks are, on their own, sufficient to support the current peak population of 15,000 oystercatchers.

20. The current peak population of 15,000 oystercatchers could not be maintained if the stocks of mussels on the regulated beds and the stocks of cockles returned to the low values seen in the early 1990s.

21. Current (or greater) stocks of wild mussels on regulated beds and cockle stocks are, on their own, insufficient to support the current peak population of 3,000 eiders. This reflects the relatively poor quality of these natural shellfish resources.

22. A healthy stock of *Ensis* (in combination with current or greater stocks of mussels on the regulated beds and healthy cockle stocks) cannot, in the absence of commercially cultivated mussel stocks, maintain the present peak population of eiders.

23. In the absence of a healthy stock of *Ensis*, the maximum peak population of eiders that the current lay mussel stock can support, is less than the current peak population of 3,000 birds.

24. The recent high peak population of eiders in The Wash probably reflects the coincidence of an unprecedented abundant stock of lay mussel resources and a peak population of the non-native *Ensis directus*. Together, these resources have the capacity to support a peak population of between 10,000 and 12,000 eiders.

25. The ability of The Wash to support the current peak population of eiders is determined by the abundance of the 'un-natural' shellfish resources ie commercially cultivated lay mussels and non-native *Ensis directus* rather than the stocks of the wild, native shellfish.

In summary, the recently observed concentration of the bulk of a large population of over-wintering eider ducks in The Wash on the Roger and Toft lays is replicated by the model. This is a foraging model, and as such the only reason for it to generate an aggregation of birds in these two locations is the presence there of a large stock of suitably sized, high quality mussels growing at a high density. The model predicts that the eiders consume c 600 tonnes of mussels from these two lays. It also predicts that, as observed, the eiders switch in late winter to feed on *Ensis directus*. The model predicts that by exploiting these two resources alone, the current peak population of c 3,000 eider ducks can be supported with only around 4 per cent being at risk of not being supported. This state of affairs depends upon the continued

availability of ‘hot-spots’ of high densities of high quality mussels such as those available on the Roger and Toft lays, and upon a continued presence of a healthy stock of *Ensis directus*. The current stock and distribution of lay mussels, in combination with a healthy stock of *Ensis directus*, has the capacity to support a far larger peak population of eider ducks than has ever been observed in The Wash. However, in the absence of either of these two resources, there is predicted to be a significant increase in the percentage of the current peak population that will be at risk of not being supported. The health of the stocks of mussels on the regulated beds and cockle beds appear to be relatively unimportant in determining the well-being of the eider population in The Wash. The ability of the shellfish resources in The Wash to sustain the current peak population of c 3,00 birds is primarily a result of the coincidence of a large stock of highly aggregated, high quality lay mussels and a healthy stock of *Ensis directus* ie the stocks of the shellfish which are not a ‘natural’ part of the Wash ecosystem.

Contents

1. Introduction

1.1 Background

The Wash is the largest estuarine system in Britain. It is fed by the rivers Witham, Welland, Nene and Great Ouse. There are extensive salt marshes, intertidal banks of sand and mud, shallow waters and deep channels. It is the most important staging post and over-wintering site for migrant wildfowl and wading birds in England. It supports a valuable commercial fishery for shellfish and also an important nursery area for flatfish. The Wash was designated as a wetland of international importance under the Ramsar Convention in 1988. It is also designated as a Special Area of Conservation (SAC) under the EC Habitats Directive and as a Special Protection Area (SPA) classified in accordance with Article 4 of the EC Directive on the conservation of wild birds (79/409/EEC), also known as the Birds Directive. The Wash is also designated as a Site of Special Sceintific Interest (SSSI), 26 per cent of which was classified as being in 'unfavourable declining' condition in the last site condition assessment. The principal reason identified for the poor condition of these areas was due to the impact of shellfishing activities on the intertidal mudflats and sandflats (lack of mussel beds following overfishing and impact of cockle suction dredging). Thus, the activities of the commercial fishery for shellfish in The Wash have been seen as the principal factors compromising the favourable condition of the site (although it should be noted the shellfish stocks are recovering following recent good spatfall and recruitment and the fisheries managers, ESFJC, are developing sustainable management measures some of which are already in use).

The Wash has supported important shellfisheries for cockles *Cerastoderma edule* and mussels *Mytilus edulis* for more than a century (Dare and others 2004). Mussel cultivation, through transplanting stocks onto 'lays' on the lower shore has also been carried out since the early 1900s (Dare and others 2004). Local fishing activities have been managed by the Eastern Sea Fisheries Joint Committee (ESFJC) since 1894 (Dare and others 2004). Since 2003, some mussel farmers on The Wash have reported high levels of mussel predation on their lays by eider ducks *Somateria mollissima*.

In order to limit this predation some lay holders applied to the Department of the Environment, Food and Rural Affairs (Defra) for a licence to shoot eiders but were first required to attempt non-lethal methods and so applied for consent from English Nature (now Natural England) to use scaring devices. However, due to the number of applications and uncertainties over the impact of scaring devices on the eiders, which are part of the SPA interest of the site, and also on non-target birds and common seal, it was not possible to show that there would not be an adverse effect on the SPA, SAC and SSSI and so English Nature refused consent. Several lay holders appealed against this decision and a public inquiry was held in summer 2006.

In advance of the public inquiry a project group consisting of Defra, fishing representatives, English Nature, ESFJC and the Marine Fisheries Agency identified a need to develop knowledge and understanding of four key areas so that objective data would be available to facilitate decision making:

1. The eider population size in The Wash.
2. The number of eiders that the site can support when the mussel and cockle beds are in favourable condition.
3. The effectiveness of scaring devices in protecting the mussel stocks.
4. The impact of the scaring devices on eiders and non-target species.

The first of these was addressed by a program of aerial surveys of The Wash conducted between November 2005 and March 2006 by the Wildfowl and Wetlands Trust (Smith, Hall, Worden, Harrison, Allen, Bradbury, Cranswick, Woodward, Shepherd, Paynter & McGill 2006). The third and fourth areas were addressed by a small-scale trial involving the use of three electronic wailers, combined with other scaring technologies, on three lays on Roger/Toft, where most predation by eiders was reported. This work was conducted by the Bird Management Unit of the Central Science Laboratories (Hart & Brown 2006). The purpose of this project is to address the second information requirement ie determining the population range of eider the site could support if shellfish stocks were in favourable condition.

Since the commissioning of this project in spring 2006, the public inquiry has taken place. The Secretary of State for the Environment, David Milliband, backed English Nature's decision to stop fishermen using electronic wailers to scare eider ducks off commercially cultivated mussel beds in The Wash. The Secretary of State accepted the Inspector's recommendation and conclusions, in particular noting that:

- disturbance from the wailers could effectively reduce the feeding and roosting areas for eiders and other waterbirds;
- displacement of birds from the vicinity of the lays could have an indirect adverse effect on the extent of natural intertidal mussel and cockle beds, and on the abundance and composition of the characterising species, such as mussels;
- the trial undertaken to assess the effectiveness of non-lethal bird scarers had concluded that wailers were of only limited effectiveness and that further research would be necessary to confirm the findings of the trial. A further study would also be required to assess the effects on individual species other than eiders.

There have not been reports of large numbers of eider in The Wash this winter. However, they could occur again, thus the results of this project, in addressing the second key area in which knowledge is lacking, will help to inform future decision making on this matter.

1.2 Aims

The principal aims of this project were as follows.

- To conduct a literature review of the current understanding of eider feeding behaviour and scoping of modelling work.

- To develop and parameterise a model of eider ducks in The Wash.
- To validate this model against independent empirical data
- To conduct model simulations of a range of alternative shellfish stock/management scenarios in order to predict their effect on the level of eider duck mortality.

These four aims are addressed in sections 2, 3, 5 and sections 4 & 6 respectively.

1.3 Method of Working

1.3.1 Initialisation of project

The first stage of this project was a start up meeting held at the offices of the ESFJC in King's Lynn in May 2006. This was attended by representatives of English Nature, Centre for Ecology and Hydrology, ESFJC and The Centre for Environment, Fisheries and Aquaculture Science (CEFAS). The first aim of this meeting was for CEH to present a version of the model to the other parties in order for them to become familiar with the model. The second aim was to establish the nature and availability of shellfish stock data that would be necessary to parameterise the model. This led to the results of recent surveys of the regulated mussel beds, cockle beds and some of the commercially cultivated mussel lays being made available by ESFJC. It was stated by one of the ESFJC officers that the biomass of the American jack-knife clam (*Ensis directus*) in The Wash may now exceed that of either mussels or cockles. Given that eider ducks exploit this resource in the Wadden See (Leopold and others in press) it was decided to include *Ensis directus* as a resource in the model. The results of recent surveys of *Ensis directus* (hereafter *Ensis*) were made available by CEFAS.

One of the principal decisions taken at this meeting was that one of the most important model outputs would be to establish the extent to which the effect on the eider population of changes to the mussel lay stock might vary, depending on the abundance/availability of other shellfish resources. It was decided that the only practical approach to achieving this was to utilise the best available estimates of the past variation in the total stock of each of the various shellfish species in The Wash to create a number of alternative scenarios in which combinations of stock levels that might occur again in the future were created. This is discussed in greater detail in section 4.

1.3.2 Literature Review

The second stage in this project was to undertake a literature review of the current understanding of eider energetics and feeding behaviour. This served four main purposes. The first objective was to build up knowledge of the way in which eider ducks forage in order to decide upon the way in which the model was structured and to determine the particular parameters that it needed to incorporate. The second objective was to derive reasonable assumptions on which the model could be based with the justification of being derived from existing studies of diving ducks. The third objective was to derive values for the many parameters that the model would need. The fourth objective was to derive independent empirical data against which model outputs could be validated prior to conducting simulations of novel scenarios. The literature review sought to gather the necessary information concerning the following aspects of eider ecology:

1. foraging behaviour

2. diving behaviour
3. food depletion
4. diving depths
5. individual variation in foraging efficiency
6. interference competition
7. diet and size selection
8. functional responses (ie intake rate in relation to food abundance)
9. constraints on food intake rates
10. assimilation and storage efficiencies
11. energy densities of food and body reserves
12. basal metabolic rate
13. energetic costs of diving
14. energetic costs of heating food
15. energetic costs of resting
16. proportion of time spent feeding
17. daily consumption of food
18. maximum daily energy expenditure
19. seasonal variation in body mass/body condition
20. over-winter mortality rates.

The full results of the literature review are not presented in text form in this report but the key findings are presented in section 3 in which the model is described. A summary of the notes concerning all of the aspects of diving duck ecology listed above that were made during the literature review are included in the appendices to this report.

1.3.3 Development/parameterisation of model

The model MORPH which is used in this project is coded in such a way that it has no system-specific features. It is entirely generic and has the flexibility to be applied to a very wide range of consumer-resource systems, subject to appropriate parameters being available (Goss-Custard & Stillman in press). The version of MORPH developed to model common scoter *Melanitta nigra* diving to feed on benthic bivalve prey in Liverpool Bay (Kaiser and others 2005) formed the basis of the version developed in this project. However, the development of a model for eiders (and oystercatchers *Haematopus ostralegus*) feeding in The Wash necessitated the formulation of a number of parameter files in order to characterise the particular species and system of interest. The development of these parameter files and the model is described in section 3.

1.3.4 Model validation/calibration

The first task after model parameterisation was to validate and if necessary calibrate the model. This was achieved by running the model to mimic current day conditions and comparing model outputs concerning the birds': distribution, feeding effort, daily energy expenditure, daily food intake, seasonal variation in body mass and over-winter mortality, against independent empirical data. It is only by conducting such a validation exercise that it is possible to establish whether, with the best estimates of parameter values and the best available knowledge concerning the biological assumptions that underlie the model structure, the model accurately mimics reality. The validation of the model is described in section 5.

1.3.5 Model simulations

The final stage of this project was to conduct the simulations and analyse the model outputs in order to explore the effects of changes to the shellfish resources in The Wash on the populations of eiders and oystercatchers, and to explore the impact of the predation pressure exerted by these birds on the shellfish resources (principally the commercially cultivated mussel lays). In the tender document for this project it was stated that "The scenarios that can be modelled will depend on the model that can be constructed using the data available….. In advance of having knowledge of the data available and the precise nature of the model, we therefore set out a provisional modelling plan….This provisional plan does not, therefore, represent a commitment to conduct all of these simulations." During the course of the project a number of changes to the original simulation plan were agreed between CEH and Natural England. The final simulation plan was agreed at a meeting held at the offices of the ESFJC in King's Lynn on the 31st January 2007. This meeting was attended by representatives from Natural England, CEH and ESFJC. Individuals representing various groups of commercial mussel growers in The Wash were invited to this meeting in order for them to provide their views on the model and to suggest scenarios that they would like to have seen simulated. However, none of these individuals attended the meeting. The final set of simulations agreed between CEH, Natural England and ESFJC is described in section 5. The results of these simulations are presented in section 6 and discussed in sections 7 and 8.

2. Literature Review

The model MORPH is coded in such a way that it has no system-specific features. It is entirely generic and has the flexibility to be applied to a very wide range of consumer-resource systems, subject to appropriate parameters being available (Goss-Custard & Stillman in press). De Leeuw (1997) developed an ecological energetic approach to elucidate the patterns in the distribution and patch exploitation of diving ducks wintering in a freshwater environment. De Leeuw (1997) stated that "It would be a challenge to extend the approach to other trophic systems for example…to other diving duck species such as eider and black scoters feeding on bivalves in the marine environment." Kaiser and others (2005) conducted a literature review to enable the model MORPH to be used to simulate common scoter feeding on bivalves in the Liverpool Bay. In the course of that literature review, over 100 scientific papers and reports concerning the physiology, diet, energetics, foraging ecology and general behaviour of diving ducks were collated. Much of the information gathered during that literature review contributed to the development of the model by Kaiser and others (2005) and hence of the model developed here. However, even the literature review conducted by Kaiser and others (2005) was far from complete, and in particular many references relating specifically to eider were not collated. The purpose of the current review was to add to the existing review by collating additional and up to date information concerning the ecology of diving ducks in general and eider ducks in particular.

In the course of the literature review approximately 100 additional scientific papers and reports were collated. During the literature review numerous notes were made of points or parameter values that may have proven relevant to the final model. These were entered into an Excel database. All of the relevant notes, together with those presented by Kaiser and others (2005) are presented in a series of appendices to this report. The full details of all the source references listed in those appendices are given in the bibliography (section 9). A written account of the literature review findings of Kaiser and others (2005) is presented in that report which is available at:

http://www.offshorewind.co.uk/Research/ResearchAreas/BirdsAndBenthos.aspx

A written report of the current literature review is not presented here but the points most relevant to the development and parameterisation of the model are discussed in the following section.

3. Development and parameterisation of the model

3.1 Background to the model MORPH

The model MORPH is the latest version in a sequence of behaviour-based models that have been developed since the early 1990s (Goss-Custard and others 1995a,b). Behaviour-based models seek to predict the population level consequences of changes to the environment on the basis of an understanding of how individuals within a population vary from one another and how, following simple behavioural rules, they interact with their environment and with one another. The models predict, on the basis of the rates with which each individual expends and acquires energy, which individuals will succeed in meeting their energy requirements and survive and which will not under any given environmental scenario. Thus, these models can be used to predict the proportion of a population that will starve under a range of alternative environmental scenarios. Various versions of the behaviour-based model have been used to model a large number of estuarine systems around the cost of England and of other countries in Europe (Goss-Custard & Stillman in press). The issues that the models have been used to address have included the impact on shorebirds of: shellfish exploitation (Burry Inlet, The Wash) (West and others 2003; Stillman and others 2003), port development (Le Seine, The Humber) (Durell and others 2005; Stillman and others 2005a), barrage construction (Cardiff Bay) (Goss-Custard and others 2006a); disturbance (West and others 2002), sea-level rise (Durell and others 2006) and improving commercial shellfish production (Menai Strait) (Caldow and others 2004). The first version of the model to address the impact of environmental change on seaducks was developed by Kaiser and others (2005) to predict the impact of off-shore windfarm development on common scoters. The development of this last version of the model provided the basis for the current model. However, to develop a version of a behaviour-based model that is specific to a particular system, the principal requirement is to characterise the distribution, abundance and quality of resources that the birds exploit within that system and also the size of the bird population exploiting those resources. These processes, as well as all of the other work involved in developing the version of the model used in this project are described in this section.

3.2 Study region

The study region with which this project is concerned is The Wash. Although a map of the entire Wash including all of its intertidal banks was used as a background map in order to visualise the distribution of birds while the model was running (Figure 3.1), the actual resources utilised by the birds in the model were restricted to the principal shellfish beds surveyed by the Eastern Sea Fisheries Joint Committee (ESFJC) and the Centre for Environment, Fisheries and aquaculture Science (CEFAS).

3.3 Global variables

Seven global variables were used in the model: day, time, day length, daylight, tide height, water temperature and air temperature. These global variables take the same value on every patch at a given point in time. Day one was taken to be the 1st of September and a model simulation covered the period from then until 31st March. Each day was divided into 24 one hour time steps. The annual maximum and minimum day length (sunrise to sunset) in The

Wash was derived from data held on the website http://aa.usno.navy.mil/cgi-bin/aa_rstablew.pl. Using a simple cosine function, these maximum and minimum values were used to calculate the duration of daylight and darkness on each day. Assuming, for simplicity, symmetry of sunrise and sunset around noon, predicted day length was used to ascribe each time step to occur either in darkness or daylight. Hourly tidal height predictions were obtained for six locations around The Wash using the Tide Wizard software (Marine Computing International 2000-2002). The average of these predicted values across the six stations was used to define the height of the tide across whole of The Wash at any given time step. Thus, the model incorporated the daily ebb and flow of the tide, the fortnightly spring-neap cycle and the annual variation in tidal height maxima and minima. Mean monthly air temperature data for The Wash for the years between 1995 and 2003 were provided by Mick Yates of CEH Monkswood. These values were averaged across years and various non-linear functions fitted to the data. A 2nd order polynomial provided the best fit to the empirical data and so this fitted equation was used to generate the day to day changes in air temperature across the whole of The Wash in the model. Mean monthly sea temperature data for The Wash for the years between 1995 and 2003 were also provided by Mick Yates of CEH Monkswood and these were analysed in the same way to generate the day to day changes in water temperature across the whole of The Wash in the model.

3.4 Patches

With the exception of the patches on which oystercatchers were allowed to exploit unspecified prey as a supplementary source of food to their principal shellfish resources, all of the patches in which the birds in the model could forage represented beds of shellfish (mussels, cockles and *Ensis* (see below)).

ESFJC provided the results of their survey of the regulated mussel beds in The Wash in autumn 2005. This listed 23 beds of which 21 were surveyed. These data were examined and the beds compared in terms of: i) the overall numerical density of mussels, ii) the cumulative size frequency distribution and iii) their geographical proximity to one another. On the basis of similarities between beds in these respects, the 23 beds were amalgamated into 12 beds for modelling purposes (Mare tail and Shellridge, Gat, Gat relay, Tofts, Herring Hill & Black Buoy, Main End, Holbeach, Trial bank, Breast, Scotsman's sled, Daseley's & Pandora, and Welland bank).

ESFJC also provided the results of their survey of 33 of the private mussel lays within the several fishery in The Wash in autumn 2005. This listed 33 lays on which the percentage cover, numerical density and hence total stock of mussels had been assessed. There are an additional 12 lays in the Wash that were not surveyed, but only two of these are of any significance and in total only constitute c 100-200 tonnes fresh mass of mussels compared to the 10,000 tonnes accounted for on the 33 lays surveyed (Ron Jessop pers. comm.) Thus, we have ignored these 12 other lays. Of the 33 lay blocks surveyed, 16 were on Toft, four on Black Buoy, one on Roger, seven on Clay Hole, four on Scotsman's sled, and one on Herring Hill. Unfortunately, data on the size frequency distribution of mussels (needed by the model) was only available from six of the lays surveyed. These beds were much more similar to one another in this respect than were the regulated mussel beds. ESFJC Research Officer, Ron Jessop stated that it was probably safe to assume that the size frequency distribution of mussels on the lays that were not sub-sampled approximated that on the lays that had been. On this basis, we have assumed that the size frequency distribution of mussel across all lays

was identical and therefore simply amalgamated the 33 blocks listed above into the six principal lay areas ie Toft, Black Buoy, Roger, Clay Hole, Scotsman's sled and Herring Hill.

Fifteen cockle beds were surveyed by ESFJC in spring 2006. These data were examined and the beds compared in terms of: i) the overall numerical density of cockles, ii) the cumulative size frequency distribution and iii) their geographical proximity to one another. On the basis of similarities between beds in these respects, the 15 beds were amalgamated into six beds for modelling purposes (Butterwick, Wrangle and Friskney, Roger/Toft, Herring Hill & Black Buoy & Mare tail & Holbeach & Gat, Inner Westmark Knock & Breast, Daseley's, and Thief/ Styleman's/ Blackguard/ Pandora). The large cockle bed on the east side of The Wash between Snettisham and Hunstanton was surveyed in June 2005 by Ecomaris Ltd (Coad & Shepherd 2005). This bed was included as a seventh cockle bed in the model.

The distribution, abundance and size frequency distribution of *Ensis directus* has been surveyed in The Wash by CEFAS on several occasions (Palmer 2003). Dave Palmer of CEFAS provided the results of the latest survey. For simplicity these data were used to define one single patch of *Ensis* in the model.

Stillman and others (2003) developed a behaviour-based model of oystercatchers in The Wash. In this model, it was recognised that upshore feeding areas on high level intertidal flats can be important to oystercatcher survival because they are exposed for longer than shellfish beds lower on the shore and hence can provide supplementary feeding when down shore areas are covered by the tide. In recognition of this, upshore mudflats were included in the present model in the form of five identical patches around The Wash in which the oystercatchers that were assumed to roost nearby could feed if necessary on the advancing and receding tide. Five additional patches were included to represent the various locations around The Wash at which oystercatchers roost at high tide (Durell & Atkinson 2004). In the light of observations by Hart & Brown (2006), it was assumed that eider ducks rest over or close to the patch on which they have been feeding most recently ie that they do not travel to a specific roosting site in The Wash. Thus, the model contained 36 patches in total that birds could utilise: six mussel lays, 12 regulated mussel beds, seven cockle beds, one *Ensis* bed, five upshore mudflats and five oystercatcher roosts.

The areas covered by each of the beds of shellfish were derived from the surveys conducted by ESFJC, CEFAS and Ecomaris. The model did not address the issue of travel costs associated with moving between patches and hence the precise location of each patch was defined simply for the purposes of creating the image of The Wash while the model was running (Figure 3.1). However, in recognition of the fact that oystercatchers in particular are known to roost at various sites around The Wash and most likely feed preferentially in close proximity to where they roost, foraging patches in the model were allocated to one of five regions in each of which there was also an oystercatcher roost. It was assumed that oystercatchers from a particular roost could travel freely between any patch within their 'home' region but would only consider travelling further afield if beginning to starve (see section 3.7.6).

3.4.1 Patch variables

Three patch variables, the value of which could differ between patches and could vary over time within a patch, were defined in the model: patch height, water depth over the patch and whether or not they were exposed.

The height of each model patch on the shore was derived as an area weighted average of the heights of each of the constituent patches as derived from the Admiralty Chart of The Wash and presented in Tables 5-7 of the Record of Appropriate Assessment (English Nature 2005). Thus, most mussel lays occurred at between +0.5 and +2.5m ODN, most regulated mussel beds occurred at between +2.0 and +3.5m ODN, and most cockle beds occurred at between +2.5 and +3.5m ODN. Upshore supplementary food patches were assumed to occur at +4.0m ODN (Stillman and others 2003). *Ensis* was assumed to occur sub-littorally and was given a patch height of -0.08m. This was the mean of the values given for the height of the lowest astronomical tide at the six tidal stations in The Wash available within Tide Wizard. The minimum tidal height in the model was +0.45m and so the *Ensis* bed was never exposed in the model. The depth of the water over each patch at each time step was calculated by subtracting the patch height from the tide height. A patch was deemed to be exposed if the water depth over a patch was calculated to be less than or equal to 0.

3.5 Resources

The literature review revealed that eider ducks eat a variety of prey items (Appendix 9). However, by far the most common type of prey is bivalve molluscs. Crustaceans, echinoderms, gastropods and worms are much less frequently recorded as prey items. References to seven species of bivalve were found within the literature review: cockles (*Cerastoderma edule*), *Ensis directus/americanus*, *Macoma balthica*, *Mya arenaria*, mussels (*Mytilus edulis*), *Spisula subtruncata* and *Venerupis pallustra*. Of these, cockles and mussels were by far the most frequently recorded prey items. Leopold, Kats & Ens (2001) stated that many Macoma will be too small to be profitable and most of the larger animals live relatively deeply in the sediment, especially in winter. On top of this, large Macoma are very hard shelled and thus take a relatively high amount of energy to be broken in the bird's stomachs (Leopold, Kats & Ens 2001). Hario & Ost (2002) also stated that Macoma seem to be an energetically poor substitute for mussels and are directly avoided by eiders in areas with access to mussel beds. Leopold, Kats & Ens (2001) stated that Mya quickly become unsuitable as prey as they become too deeply buried and too large to swallow. They found very few studies where feeding on Mya was observed on more than a very limited scale. This dietary information, coupled with the abundance and well surveyed stocks of mussels, cockles and *Ensis directus* in The Wash, resulted in these three prey species being the only food resources included in the model (apart from a supplementary upshore resource made available to oystercatchers only (Stillman and others 2003).

Each of these three principal prey resources was divided into a number of size classes in order to take account of the fact that eiders and oystercatchers consume different prey size ranges (Table 3.1) and that in all cases the energetic profitability of bivalves varies with their length.

Table 3.1 Summary of the size class ranges of shellfish consumed by eider ducks. Information derived from the literature review (Appendix 9).

	Cockles	*Ensis*	Mussels
Minimum size ever recorded	5mm – 10mm	41mm - 45mm	1 mm
Most frequently recorded minimum size	15mm – 20mm		11 mm
Most frequently recorded maximum size	35mm – 40mm		47 mm
Maximum size ever recorded	45mm – 50mm	140 mm	80mm
Notes	Select against those > 40mm	Select larger rather than smaller ones	

As in previous models (Stillman and others 2003), oystercatchers were assumed to consume cockles between 15mm and 45mm and mussels between 20mm and 70 mm. Thus, mussels between the sizes of 5 mm and 70mm were included in the model and were represented as thirteen 5 mm size classes ie 5mm -10 mm, 10mm – 15mm etc. Cockles between 5mm and 45mm were represented by eight 5mm size classes. In the surveys of *Ensis directus* by CEFAS (Palmer 2003) *Ensis* between 45mm and 110mm shell length were found. Eiders are known to consume *Ensis directus* up to 140mm (Leopold and others in press). Thus, *Ensis* was represented in the model as five size classes ie 40mm – 50mm, 50mm – 70mm, 70mm – 90mm, 90mm – 110mm and over 110 mm. For simplicity, the supplementary food resource that was made available to oystercatchers feeding on upshore flats was represented as a single resource on which oystercatchers were assumed to achieve the observed average overwinter intake rate from upshore areas ie 0.67mg ash free dry mass per second (Stillman and others 2003). Thus, there was a total of 27 resources that birds in the model could potentially feed upon.

These resources were amalgamated into diets. Many studies of eider ducks stress the importance of the flesh:shell ratio, which varies with the length of the bivalve, in determining the energetic profitability of food to eider ducks which ingest their prey whole (Guillemette 1994; Nehls 1995; Bustnes 1998). Subtle differences in flesh contents and shell masses between different size classes govern the birds' feeding decisions over winter (Leopold, Kats & Ens 2001). In many locations flesh content will be too low and shells too thick to allow a sufficient energy gain. In fact eiders feeding on poor mussels may in theory starve despite having a full stomach (Nehls 2001). Bustnes & Erikstad (1990) observed that the most frequent size of mussels (7mm - 23mm) eaten by common eider in Norway corresponds to the highest flesh:shell ratio and showed that, when consuming mussels larger than 25mm, the quantity of mussels required per day increased the shell intake. For this reason, it was decided to allocate each of the mussel and cockle resources into one of two diets available to eiders ie small (5mm - 25mm) or large mussels (25mm - 50mm) and small (5mm - 25mm) or large cockles (25mm - 45mm). This allowed eiders to choose between exploiting different sized prey resources rather than forcing them to feed on all mussels or cockles on a given patch. This could have reduced the average quality of the prey available on a patch to a point where

the resource was not profitable. It was decided to combine all of the *Ensis* size classes into a single *Ensis* diet on the basis that the shell mass of *Ensis* changes relatively little with length in comparison with cockles and mussels (Fig 3.2). As oystercatchers do not consume the shell of cockles or mussels, this issue was not relevant and so all cockles and mussels within oystercatchers' known exploited size range (cockles – 15mm - 45mm, mussels 20mm - 70mm) were allocated to the same diet ie a cockle diet or a mussel diet.

The initial numerical density (individuals m^{-2}) of each resource on each patch was derived from surveys of the shellfish stocks of The Wash provided by the Eastern Sea Fisheries Joint Committee (ESFJC) and the Centre for Environment, Fisheries and Aquaculture Science (CEFAS).

3.5.1 Regulated mussel beds

The results of the survey of the 23 regulated mussel beds conducted by ESFJC in autumn 2005 were examined and where beds had been combined to yield the 12 beds used in the model, average numerical density for each mussel size class (weighted by the areas of each of the beds that had been combined) was calculated.

3.5.2 Mussel lays

The results of the survey of the mussel stocks on 33 mussel lays conducted in autumn 2005 by ESFJC were used to derive the numerical density of each size class of mussels on each of the six model lays. In most cases, the data available for each lay consisted of the biomass of live mussels per 0.1 m^{-2}. We have assumed that the results of the limited size-frequency distribution sampling that was done applied to all lays. An overall figure for the numerical density of mussels on each lay was guessed and progressively modified until the resultant overall biomass density on each lay (resulting from that assumed overall numerical density value, in combination with the size frequency distribution and masses of individual mussels of different sizes), matched the value provided by ESFJC. In this way an estimate of the numerical density of each size class of mussels on each lay was derived.

3.5.3 Regulated cockle beds

All 15 of the principal cockle beds of The Wash were surveyed by ESFJC in spring 2006. Only six of these were surveyed in autumn 2005. In each case, values for the area of the bed covered by juvenile (<=14mm) cockles and fishable cockles (> 14mm) was available as was an estimate of the numerical density of each 5mm size class. For those beds that were surveyed in autumn 2005, these values were used to derive weighted mean numerical densities of each size class across the whole bed. For those beds that were not surveyed in autumn 2005 it was necessary to back-predict what the numerical densities on those beds would have been in autumn 2005. This was done by first calculating an average overwinter (autumn 2005 – spring 2006) proportionate change in the numerical density of each size class on each of the beds that had been surveyed on both occasions. For those beds that had not been surveyed in autumn 2005, the spring 2006 numerical density of each size class were then divided by the appropriate size-specific proportion to yield an estimate of the numerical density of that size class on each bed in the preceding autumn. These values were then combined with the actual autumn 2005 survey results on the other beds and weighted average numerical densities of each size class calculated for six of the cockle beds in the model.

3.5.4 Private cockle fishery

The 7th cockle patch is a private fishery not managed by ESFJC. It is a large cockle bed on the east side of The Wash between Snettisham and Hunstanton and was surveyed by Ecomaris Ltd. in June 2005 (Coad & Shepherd 2005). The survey yielded estimates of the numerical density of each of the size classes of cockles on that patch.

3.5.5 Ensis beds

Dave Palmer of CEFAS provided the results of the most recent survey of the stocks of *Ensis directus* in The Wash. This identified eight areas in which *Ensis* was found and the numerical density of each of the 5 mm size classes between 45 and 110 mm was recorded on each patch. For simplicity, these size classes were combined into five size classes and the (area) weighted average numerical density of each size class calculated across the whole area in which *Ensis* was found. These values were used to characterise the resources available on the single patch of *Ensis* included in the model. The initial numerical density of resources on the upshore supplementary feeding area made available to oystercatchers (assumed to equate to various species of worm and bivalve eg *Macoma balthica* that oystercatchers typically exploit in such places) was set to a very high value such that it was effectively a non-depleting resource on which birds could (if necessary) attain a fixed but low intake rate throughout the winter as a supplement to the intake rate achieved on their principal low-water feeding areas. This is the same approach to modelling this type of resource as has been used in several previous models of oystercatchers (Stillman and others 2000a, 2003).

All of the above relates to the derivation of the initial autumn numerical density of each resource on each patch. The model itself calculates the overwinter depletion of each of the resources due to consumption by the birds. However, this is not the only overwinter source of change to the numerical densities of shellfish. Consumption by other predators and other sources of natural mortality, as well as the growth of individuals may see the abundance of some size classes decline while others increase. It was necessary to include these 'background' changes in the model. As there were no data on the numerical densities of mussels stocks in The Wash in spring 2006 from which it might be possible to work out the over-winter change, we used published values of the over-winter mortality rate of mussels due to factors other then bird predation ie 7 per cent per winter for each size class (Stillman and others 2000a) and applied this to all size classes of mussels on all regulated beds and lays. Analysis of the surveys of cockles on six beds in autumn 2005 and spring 2006 yielded estimates of the average (across beds) proportionate overwinter change in the numerical density of each of the size classes. This revealed a linear relationship between cockle size and over-winter proportionate change in numerical density: the smallest size classes declined markedly in abundance, while the largest increased (Figure 3.3). It should be noted that these figures are not derived from cages from which bird predators have been excluded and so losses due to birds may be included in these values. However, the value of -71 per cent for the smallest cockles is similar to the value of -60 per cent for first winter cockles cited from Hancock (1971) by Stillman and others (2001). Stillman and others (2001) sourced a value of 10 per cent overwinter mortality for larger cockles from Horwood & Goss-Custard (1977). This is pessimistic compared to the gains apparent amongst the larger size classes between autumn 2005 and spring 2006. However, there is consistency between the results derived here and those presented by Stillman and others (2001) in that it is the abundance of the smallest cockles that declines most dramatically over-winter. Where repeat surveys of a given cockle bed in autumn 2005 and spring 2006 permitted bed-specific rates of change to be derived,

these were used in the model, otherwise the across-bed average changes in the numerical abundance of cockles of each size-class were assumed to apply across the other cockle beds in the model.

There were no data concerning the overwinter change in the numerical density of *Ensis directus* in The Wash. Thus, we used estimates of the size-specific overwinter change in the numerical abundance of razor clams derived from work in Liverpool Bay (Kaiser and others 2005) to approximate the situation in The Wash. These data indicated that the smallest razor clam size class declined in abundance by c 20 per cent while the larger size classes increased in abundance by around 8 per cent. This may reflect overwinter growth of these sub littoral bivalves.

3.6 Components

Four resource components which influence the energetic profitability of consuming a given type and size of bivalve are considered in the model ie the ash free dry flesh mass (AFDM), shell mass, water mass and salt content of a prey item. The AFDM of marine invertebrates varies between 75 per cent and 90 per cent of the dry flesh mass (Zwarts and others 1996a). We used a value of 84 per cent (the mean value for bivalves) to convert AFDM to dry flesh mass (Ricciardi & Bourget 1998). It is assumed that birds only assimilate energy from the ash free dry mass component of their food. Although shell and water are not components from which foraging birds gain any energetic benefit, the model included a measure of these because the gut capacity of the birds is dictated by the volume of fresh prey mass that they ingest, not by the volume of dry matter from which they extract energy and nutrients. In the case of eiders which consume their prey whole, gut capacity is dictated by the mass of whole live animals ingested. In the case of oystercatchers which remove the shell of shellfish before consuming them it is only the volume of the wet flesh that fills the gut. Nystrom, Pehrsson & Broman (1991) noted that the seawater content of a mussel is positively correlated with its size and the excretion of excess salt by the foraging bird imposes extra energetic costs. Nehls (1995) noted that salt intake incurs an energetic cost of salt turnover that can equate to between 2.4 per cent and 3.1 per cent of the metabolizable energy intake depending on mussel size. Thus, it was necessary to include the salt as a resource component which actually reduces the energy that a bird has at its disposal.

Ideally, species specific relationships between the mass of each component contained within an individual bivalve and its length would have been derived from samples collected in the autumn in The Wash. Unfortunately, this was not available and it was necessary to collate/derive the necessary mass-length relationships from a number of sources as detailed in Table 3.2. The relationship between shell mass and length is presented (Figure 3.2) as an example of the relationships detailed in Table 3.2. This figure highlights the considerable difference between the various shellfish resources in terms of their shell content and hence profitability to eider ducks. For a given length of bivalve, cockles contain considerably more shell mass than mussels or *Ensis*. Among mussels, those from natural mid-shore mussel beds have greater shell content than equivalently sized mussels from low-shore commercially cultivated lays. *Ensis*, because of their different shell geometry, have the least shell mass of all for a given shell length. The equations detailed in Table 3.2 were used to derive the predicted mass of each component in each size class of each prey species in the model.

All of the above relates to the derivation of the initial autumn component density of each resource. In order to incorporate the known over-winter decline in the flesh content of mussels and cockles, existing values from previously published studies were used. Stillman and others (2000a) give a value of a 40 per cent decline in the flesh content of mussels over-winter. This was confirmed with data from lay mussels gathered in the Menai Strait (R. Caldow unupbl. data.). Stillman and others (2001) give a value of 50 per cent for the over-winter decline in the flesh content of cockles. These values were applied to all size classes of mussels and cockles on all patches in the model. They were applied equally to both the ash free dry mass component and the water mass component such that the fresh flesh mass declined by the requisite amount. An analysis of relationships between ash free dry mass and shell length of razor clams from Liverpool Bay in August, December and April revealed that in contrast to mussels and cockles there is no marked over-winter change in the flesh content of these sub littoral bivalves ie +/- 5 per cent compared to -40 per cent to -50 per cent. Thus we have assumed that *Ensis* in The Wash do not exhibit any seasonal decline in flesh content over the winter.

Table 3.2 Equations relating the mass of each component held within a prey item belonging to each shellfish resource in the model to its length.

Component	Resource	equation	source
Ash free dry mass	mussels (lays)	AFDM(mg) = exp(-30.63 + 15.3 * ln length(mm) - 1.479 * Ln length(mm) sq + 0.156/2)	1
	mussels (regulated)	AFDM(mg) = exp(-30.29 + 16 * ln length(mm) - 1.673 * ln length (mm) sq + 0.0744/2)	2
	cockles	AFDM(mg) = exp(-4.375 + 2.910 * ln length(mm) + 0.0534/2)	3
	Ensis	AFDM(mg) = 1000*exp(-13.5 + 3.01 * ln length(mm) + 0.21/2), AFDM(mg) = 1000*(-14.2 + 3.15 * ln length(mm) + 0.24/2)	4
Shell dry mass	mussels (lays)	Shell(mg) = exp(-3.117 + 2.990 * ln length(mm) + 0.0246/2)	5
	mussels (regulated)	Shell(mg) = exp(-3.378 + 3.161 * ln length(mm) + 0.0163/2)	6
	cockles	Shell(mg) = exp(-2.087 + 3.141 * ln length(mm) + 0.0274/2)	3
	Ensis	Shell(mg) = 1000*exp(-12.05 + 3.01 * ln length(mm) + 0.08/2), Shell(mg) = 1000*exp(-12.4 + 2.93 * ln length(mm) + 0.1/2)	4
Water mass	Mussels (lays & regulated)	Water(mg) = 1000*exp(-8.503+2.703*ln length(mm))	7
	cockles	Water(mg) = exp(-1.510 + 2.844 * ln length(mm) + 0.0143/2)	3
	Ensis	Water(mg) = (AFDM(mg)/0.1186)-AFDM(mg)	8
Salt mass	All resources	Salt(mg) = AFDM(mg) * (0.52 -0.004*length(mm))	9

Sources:

1. Derived from low-shore intertidal lay mussels from Menai Strait in October 2000
2. Derived from mid-shore intertidal natural mussel beds in the Menai Strait in October 2000
3. Derived from cockles collected from Wrangle, Heacham and Mare's tail in October 2004
4. Two equations derived from samples of razor clams gathered from i) Shell Flat and ii) Llandulas in Liverpool Bay in August 2003. The mean of the values predicted by these two equations was used as the predicted value in the model.
5. Derived from low shore intertidal lay mussels from Menai strait in March 2002
6. Derived from mid-shore intertidal natural mussel beds in the Menai Strait in March 2001

7. This is the equation presented by Nehls (1995). However, this equation was not used to calculate water contents of mussels directly in the model. Rather, it was used, in combination with three autumn equations relating AFDM to shell length for mussels from the same location also presented by Nehls (1995 Table 5.3), to calculate size specific values for the wet flesh mass (sum of AFDM/0.84 and water content) and thence size specific values for the proportion of the wet flesh that comprised AFDM. From these values it was then possible to back calculate from the values of AFDM predicted by the equations 1 and 2 above, the wet flesh mass and hence the water content of the mussels. In this way the relative magnitude of the predicted water and flesh content of the mussels in the model was generated from one set of mussels (those of Nehls (1995)) rather than combining absolute measures of flesh content from Menai Strait and of water content from Konigshafen.
8. Water content of *Ensis* derived on the assumption that the AFDM comprises 0.1186 of the wet flesh, this being the mean value derived across all sizes of mussels in the model (see note 7).
9. Derived from equations relating the salt content (g salt per g AFDM) to shell length of mussels presented by Nehls (1995) (Fig 6.1 (mean of the coefficients for January 1992 and January 1994)

3.7 Foragers

3.7.1 Types and numbers

Two types of foragers are represented in the model: eider ducks and oystercatchers. Eiders are the principal focus of this study. Oystercatchers were included for two reasons. First, the areas supporting commercially cultivated mussel lays support a significant proportion of the oystercatcher population of The Wash (English Nature 2005). Thus, the changes to the scale of the commercially cultivated lays explored in the model simulations could have an affect on the oystercatcher population. Second, oystercatchers are direct competitors with eider ducks for the two key food resources of mussels and cockles. By virtue of the depletion of shellfish stocks that they generate, oystercatchers may have a marked influence on the size of the eider population that the shellfish stocks of The Wash can support.

Eider numbers counted under the WeBS scheme have fluctuated greatly on a year-to-year basis over the last 40 years (Figure 3.4). Corrected WeBS count data for the winter of 2005-2006 were, however, not available at the time of model parameterisation. Moreover, because WeBS counts are land-based, they are subject to a number of sources of error when used as an assessment of the size of sea duck populations that occur offshore. WeBS counts are: limited in their seaward extent; affected by the weather-dependent suitability of viewing conditions over long distances; and constrained by the limited time available necessary to make the lengthy scans of the sea needed to record sea duck numbers accurately (Smith, Hall, Worden, Harrison, Allen, Bradbury, Cranswick, Woodward, Shepherd, Paynter & McGill 2006). In recognition of these limitations, aerial surveys of The Wash were conducted in 2005-2006. A peak of 2,358 eider was counted during the aerial survey in January 2006 (Smith, Hall, Worden, Harrison, Allen, Bradbury, Cranswick, Woodward, Shepherd, Paynter & McGill 2006). In January and February 2006 Hart & Brown (2006) regularly counted in the region of 3,000 birds within the area around the Roger and Toft lays. Numbers in the winter of 2005-2006 were clearly high and we have assumed a peak over-winter population of 3,000 eider ducks in the model.

In contrast to the apparently large year to year fluctuations in the number of eider ducks, the peak overwinter count of oystercatchers has been relatively stable (1999-2000 – 15,701, 2000-2001 – 13,457, 2001-2002 – 13,371, 2002-2003 – 16,760, 2003-2004 – 14,684). The mean of these values is 14,795. The peak count from the winter of 2005-2006 was 14,705 in December 2005. We have therefore assumed a peak oystercatcher population of 15,000 birds in The Wash. The model was run with 300 ‘super-individuals’ of both eiders and oystercatchers, representing 10 and 50 real birds respectively.

3.7.2 Forager Constants

Arrival day and region and departure day Neither the population of oystercatchers nor eiders remains at the peak size for the entire over-wintering period. Thus, it was necessary to incorporate the seasonal patterns of arrivals and departures to and from The Wash by both species.

Oystercatchers WeBS count data reveal that the peak oystercatcher population in The Wash usually occurs in January. Nationally, 80 per cent of the peak overwinter count of oystercatchers is already present in September and approximately half of the birds have left by March. Thus, in the model it is assumed that 12,000 oystercatchers are in The Wash at the start of the model run, that the remaining 3,000 birds arrive between October and January and that 50 per cent of the birds leave between mid February and mid March.

The Wash is a large geographic area and oystercatchers are known to roost at high tide at a large number of sites around its margins (Durell & Atkinson 2004). It is highly likely that under most circumstances birds will feed at low water on the sand and mud flats nearest to their roost site rather than flying large distances to other parts of The Wash nearer other roosts. In the model we therefore assigned each oystercatcher to arrive in and to stay within one of five regions of The Wash: the west(north) (Friskney & Wrangle), the west(south) (Butterwick & Freiston), the south(west) (Holbeach), the south(east) (Terrington) and the east (Snettisham & Heacham). The results of the over flights of The Wash in 2005-2006 were examined and the mean proportion of oystercatchers found in each region across the five surveys was calculated. These proportions were used to allocate oystercatchers to the five regions of The Wash. This allocation **did not** dictate where within each region the birds fed. Moreover, we assume that when an oystercatcher's mass falls below 75 per cent of its target mass, it is free to move to any of the other regions in The Wash in search of better foraging conditions (see section 3.7.6).

Eiders The aerial surveys of The Wash conducted between November 2005 and March 2006 (Smith, Hall, Worden, Harrison, Allen, Bradbury, Cranswick, Woodward, Shepherd, Paynter & McGill 2006) revealed that approximately 50 per cent of the peak numbers counted in January were present in November and that by March the peak number had declined by approximately 50 per cent to return to the numbers present in November. Examination of the monthly count data from The Wash over several years since 1996 indicates a similar pattern (English Nature 2005). These data suggested that the population size in September and October is on average around 25 per cent of the peak winter count. Thus, in the model, 750 eiders (25 per cent of the peak count of 3,000) are assumed to be present at the start of the run. A further 750 birds are assumed to arrive between mid October and mid November and the remainder to arrive between mid December and mid-January. Half of the peak population is assumed to leave between mid January and mid February.

There is no data concerning the distribution of roosting eiders in The Wash. In theory, eiders can roost on the water over their feeding grounds wherever they happen to be. Hart & Brown (2006) noted that eiders do indeed tend to aggregate into rafts at high water close to their feeding grounds Thus, we have assumed that eiders, unencumbered by the need to return from a feeding area to a specific roost site on a beach, can feed and roost anywhere within The Wash and will therefore roost at their most recent feeding location.

Feeding efficiency Individual variation in the intake rate of foraging animals arises largely from variation in two individual characteristics: i) foraging efficiency, their intake rate in the absence of conspecifics, and ii) susceptibility to interference, the immediate and reversible detrimental effect on their intake rate caused by the presence of competitors (Goss-Custard & Durell 1987; Goss-Custard & Sutherland 1997; Caldow and others 1999; Stillman and others

2000b). There is very little information concerning variation in foraging efficiency between individual diving ducks. Tome (1988) compared the slopes and intercepts of the energy gain functions among individual ruddy ducks *Oxyura jamaicensis* within a patch density and found no difference in slopes or intercepts. However, in terms of optimal foraging efficiency (ie when birds chose to leave patches) Tome (1988) found that this differed between individual ruddy ducks - some birds behaved closer to optimality than others. In studies of tufted ducks *Aythya fuligula* Draulans (1984, 1987) found that among four captive ducks the most profitable size class of mussel varied between 12.5mm - 15mm and 20mm - 22.5mm. Draulans (1984, 1987) concluded that this variation can only stem from variation in the speed with which different birds handled mussels of different sizes. Nehls (1995) found pronounced variation between five captive eiders in the relationship between mussel handling time and mussel length when offered loose mussels on a tray. Thus, although there is little quantitative data it is likely that eider ducks in the wild do indeed vary considerably in their feeding efficiency.

In contrast to diving ducks, there is good experimental evidence of considerable variation in the feeding efficiency of captive dabbling ducks (Fritz, Durant & Guillemain 2001; Durant and others 2003). However, perhaps the best example of the quantification of the variation in feeding efficiency between individual birds feeding on bivalve prey in the wild is that of colour-ringed oystercatchers feeding on intertidal mussel beds (Goss-Custard and Durell 1987). In this case, the standard deviation in feeding efficiency around the population mean value is around 12.5 per cent of the mean value (Stillman and others 2000b). Given the fact that captive tufted duck and eider feeding on mussels exhibit individual variation in their feeding efficiency, much as oystercatchers do, the model assumes that the variation in feeding efficiency amongst eiders feeding on benthic bivalves is of the same magnitude as that of oystercatchers feeding on benthic bivalves. Thus, the feeding efficiency of each individual within the populations of both eiders and oystercatchers is drawn from a normal distribution, with a mean of one and a standard deviation of 0.125.

Dominance The dominance of each individual within the populations of eiders and oystercatchers is drawn at random from a uniform distribution of scores between a minimum of zero and a maximum of one. This value had no bearing on the fate of individual eiders as we have assumed no interference between foraging eiders (see below) but will have had an effect on the susceptibility of each individual oystercatcher to interference competition and thus their probability of survival (see below).

Threshold density for interference The influence of conspecific competitors on a bird's intake rate was incorporated using the following interference function (Stillman and others 1996).

$$IR = IFIR\left(\frac{gD+1}{D_0+1}\right)^{-(m_{\max}-(m_{\max}-m_{\min})d)} \qquad \text{if } D \geq D_0$$

$$IR = IFIR \qquad \text{if } D < D_0$$

where IR = intake rate (mg s^{-1}), $IFIR$ = Interference-free intake rate (mg s^{-1}), D = conspecific competitor density in patch (hectares^{-1}), D_o = conspecific competitor density above which interference reduces intake rate, g = aggregation factor, d = dominance of focal individual (0-

1), m_{max} = susceptibility to interference of least dominant individual ($d = 0$) and m_{min} = susceptibility to interference of most dominant individual ($d = 1$). D_o was set to 100 birds hectare^{-1} for oystercatchers as this is the approximate threshold in a number of systems in which interference occurs through either kleptoparasitism (Stillman and others 1996; Triplet, Stillman & Goss-Custard 1999) or a reduction in prey availability due to prey avoidance behaviour (prey depression (eg Yates, Stillman & Goss-Custard 2000)). In the case of eiders D_o was set to a very high number in order that it was never exceeded in the model ie depression of intake rate due to interference was not assumed to occur among eiders (section 3.7.3).

Lower critical temperature The lower critical temperature (below which thermostatic energy costs are incurred) for oystercatchers was calculated from the relationship between known values for various wader species (from a literature search) and body mass (Stillman and others 2005b). This yielded a lower critical air temperature of 10^{o}C for oystercatchers. The lower critical temperature for eiders (in water) is 15^{o}C (Jenssen, Ekker & Bech 1989).

3.7.3 Forager variables

The model defined six forager variables ie characteristics ascribed to each forager which vary in space and time depending upon where and when it forages. Four of these applied only to eider ducks and define the time per dive that is spent: i) underwater, ii) travelling between the sea surface and the seabed, iii) on the surface before the next dive and iv) foraging on the seabed. Together, these four variables constitute the diving sub-model. One other variable (the susceptibility to interference) was used in calculating the reduction in intake rate suffered by individual oystercatchers given the number and status of conspecifics on the same patch (see below). This variable applied only to oystercatchers. The final forager variable was the degrees Celsius below the lower critical temperature.

Diving sub-model This is described in detail by Kaiser and others (2005). The basis for this model is the dataset collated by Dewar (1924) on a number of diving duck species. This dataset contains relationships between the depth of the water and the length of time spent underwater per dive and on the surface between successive dives. Assuming an average speed of travel while underwater (derived from the literature review) it is possible to estimate the time spent travelling to and from the water surface as a function of water depth and thence, by subtraction from the total dive time, the amount of time on the seabed per dive. This latter variable can then be divided by the sum of the dive duration and the surface pause duration to yield an estimate of the proportion of each dive cycle that is spent on the bottom as a function of water depth. These relationships are depicted in Figure 3.5. Subsequent to the review of Kaiser and others (2005) two further empirical studies of the diving behaviour of eiders have been found (Ydenberg & Guillemette 1991 and Guillemette and others 2004).Broadly speaking, the diving sub-model as represented in MORPH gives similar results to those of the two empirical studies. For example, a comparison of the relationship between the amount of time spent on the bottom and water depth as represented in MORPH and as derived from the study of Guillemette and others (2004) is shown in Figure 3.6. A further comparison of the relationship between the amount of time spent on the surface between successive dives and the depth of the water in which a bird is diving as represented in MORPH and as derived by a combination of relationships presented in Guillemette and others (2004) and Ydenberg &

Guillemette (1991) is shown in Figure 3.7. Given the similarity between the relationships generated by the diving-sub model and these independent empirical studies of the diving behaviour of eiders we decided to retain the diving sub-model as described in detail by Kaiser and others (2005).
In essence the model predicts that as water depth increases the total time spent underwater per dive increases up to a maximum dive duration of 60 seconds. This compares with the aerobic dive limit of eiders which is estimated to be 51 seconds (Hawkins and others 2000) and the mean of 12 published values for the maximum dive duration of eiders ie 53.3 seconds. In the model this limit is reached at a depth of 9m. The maximum depth of water in the model of The Wash is 8.12m which occurs at high water on spring tides over the subtidal *Ensis* beds (assumed to occur at mean LAT ie -0.08m). Thus, the issue of constraining dive durations to an upper limit does not in fact arise in this model (unlike that of the model of common scoters diving in up to 25m of water in Liverpool Bay (Kaiser and others (2005)). As water depth increases, so too does the travel time, but because this increases at a slower rate than dive duration, the amount of time spent on the bottom increases per dive up to a depth of c 10m. The amount of time spent on the surface between successive dives increases steeply with increasing water depth, again up to a depth of 9m. Consequently, the proportion of each dive cycle (ie underwater time + surface time) that is spent on the bottom gathering food decreases steadily with increasing water depth (Figure 3.5). Because eiders in The Wash frequently feed by up-ending and dabbling in shallow water (Hart & Brown 2006) it is important to consider how the model predictions work out as water depth approaches 0m. The model predicts that as the water depth approaches 0m a foraging eider will spend c 60 per cent of its time with its head underwater gathering food. It is assumed that this is not an unreasonable estimate given that birds cannot dabble continuously but must lift their head periodically between dabbling bouts. The model assumes that eiders cannot forage once water depth falls to 0m ie once a patch is exposed by the tide.

Susceptibility to interference The reduction in the instantaneous intake rate achieved by oystercatchers due to interference when densities of conspecific competitors exceed the threshold density was calculated from the equation given in section 3.7.2.. The aggregation factor accounts for the fact that birds will usually be aggregated in a patch, rather than being spread uniformly. The default aggregation factor for oystercatchers was assumed to be 10, the value measured for cockle-feeding oystercatchers on the Burry Inlet, UK (West and others 2003). The strength of interference between oystercatchers foraging on both cockles and mussels (m_{max} = 0, m_{min} = 0.5) was that observed for birds feeding on low (c 250 cockles m^{-2}) cockle densities in the Baie de Somme, France (Triplet, Stillman & Goss-Custard 1999) and represents a strong level of interference amongst shellfish feeding oystercatchers. This is the strength of interference assumed in the model of shellfish eating oystercatchers on the Exe estuary (Stillman and others 2005b). Triplet, Stillman & Goss-Custard (1999) recorded much weaker interference amongst cockle feeding oystercatchers, but only when cockle densities were an order of magnitude higher ie 2,500 m^{-2}. As the greatest bed-wide average cockle density on any of the cockle beds in the autumn 2005 surveys of The Wash was c 500 m^{-2} there was no justification for assuming that interference amongst cockle feeding oystercatchers would be weak in the model.
Nehls (1995) suggested that social interactions appeared to limit the densities of foraging eiders on the preferred feeding grounds. Piersma & Camphuysen (2001) suggested that the combined fisheries activities in the Wadden Sea resulted in a reduction of the foraging range of eiders by the removal of old natural mussel banks, the partial removal of high density cockle and Spisula banks and a shift towards mussel cultures. They suggested that this would

then have led to increased levels of interference and a reduction in the carrying capacity of the Dutch Wadden Sea. However, neither they nor Nehls (1995) present any evidence to support the existence of interference amongst foraging eiders. Of all the c 200 papers read in the current literature review and that of Kaiser and others (2005) only one (Ashcroft 1976) provides any direct evidence of interference amongst foraging eiders. Ashcroft (1976) compared the mean feeding rate (items/min) achieved by female eiders in medium density flocks (2.62 items/ min) and high density flocks (2.20 items/ min) and found a 16 per cent drop in achieved feeding rate with increasing density. However, Ashcroft (1976) gave no indication as to what constituted medium and high densities. Goudie & Ankney (1986) measured the aggressive behaviour of common eiders in winter and found that it was negligible compared to other sea duck species. Observations of the foraging behaviour of eider indicate that interference competition arises and takes the form of intraspecific kleptoparasitism ie theft of individual prey items, when they forage in Agarum beds in search for spider crabs, a rare prey species of a high energetic value (Guillemette & Himmelman (1996). However, interference competition is absent when eiders are searching for blue mussels in kelp beds (Guillemette, Ydenberg & Himmelman 1992). Furthermore, in 80 per cent of 159 repeat surveys of the eider population distribution across 13 mussel beds, Guillemette and others (1993) and Guillemette & Himmelman (1996) found that as the eider population varied between 10 and a few thousand birds, only one or two patches were used. Eiders crowded increasingly into the one or two favoured patches as the population increased. In the light of this, Guillemette & Himmelman (1996) discarded the possibility that interference was driving the distribution of wintering eiders. It is possible to estimate from the maximum population category (>3,200 birds) and the size of the two most popular beds (4.67ha) in the studies of Guillemette that the maximum observed density of eiders across the two beds used at high population sizes was circa 685birds/ hectare. If all of the 3,000 eiders in The Wash were to aggregate onto the Roger Lay alone (35ha), the maximum density would be only 86birds/ hectare. This is far below the densities observed by Guillemette and others (1993) and Guillemette & Himmelman (1996). Given this fact, the lack of evidence of interference amongst mussel feeding birds found by Guillemette, Ydenberg & Himmelman (1992), and the complete lack of any quantitative relationship between the intake rate achieved by eiders and the density of the flock, we conclude that there is little reason to include interference between foraging eiders in the model.

Degrees below lower critical temperature This was calculated simply be deducting the current ambient water (in the case of eiders) or air (in the case of oystercatchers) temperature from the lower critical temperature for each species. The magnitude of the difference affected the rate at which birds metabolised energy (see below). If the ambient temperature exceeded the lower critical temperature this variable was set to 0.

3.7.4 Rate of acquisition of energy

Rate of consuming each diet The rate at which a bird can acquire resources over a period of time depends upon the length of time for which the resources are available to it during that time and the 'instantaneous' rate at which they can consume resources while the resources are available to them. In the case of oystercatchers these equate to: i) the length of time for which the patch is exposed by the tide and ii) the 'instantaneous' rate at which prey are consumed while foraging on the patch. In the case of benthic feeding diving ducks these equate to: i) the

proportion of a dive cycle that is spent on the bottom and ii) the 'instantaneous' rate at which prey are gathered while on the bottom. Whether a patch is exposed or not and hence available to oystercatchers or eiders is determined by the rise and fall of the tide in the model and the patch heights (section 3.4.1). The proportion of a dive cycle that is spent on the bottom by an eider duck is calculated as described above (section 3.7.3). In both species, the second factor ie the 'instantaneous' rate at which they gather prey while in contact with the foraging substrate, can, as in most foraging animals, be related to the density of prey items available to them. This relationship is termed the functional response. The way in which the functional responses of oystercatchers and eiders were derived is described here.

The interference free intake rate achieved by an average oystercatcher while foraging on either mussels or cockles was calculated from a generic equation in which the coefficients describing the asymptote of the functional response attained at high prey density and the prey biomass density at which intake rate is 50 per cent of this asymptotic value (ie the gradient of the functional response) were derived from statistical models fitted to empirical data concerning waders (Stillman and others 2005b; Goss-Custard and others 2006b). This average value was then multiplied by the foraging efficiency and susceptibility to interference of each individual to yield variation in the instantaneous intake rates achieved by birds within the population. Intake rates were multiplied by zero if a patch was covered by the tide to prevent oystercatchers from feeding in such places at such times. All oystercatchers, independent of their foraging efficiency or susceptibility to interference were assumed to attain a fixed intake rate of 0.67mg AFDM sec^{-1} when feeding on the supplementary prey diet. This is the mean value measured empirically in a number of studies and used in the model of oystercatchers in The Wash developed by Stillman and others (2003). This generic approach to predicting the intake rates achieved by oystercatchers feeding on various resources has been applied in many of the previous models of this species (Stillman and others 2005b).

In estimating the functional response of common scoters, Kaiser and others (2005) took the mean of the gradients and asymptotes of four slightly differing functional responses presented by Richman & Lovvorn (2003). These were derived from observations of captive velvet scoter *Melanitta fusca* feeding on Macoma spp. of differing sizes and buried to different depths. This yielded an asymptotic intake rate of 0.52 bivalves sec^{-1} ie a handling time of c 2 seconds per prey item. However, in the case of eiders feeding on mussels, most of the handling time is spent loosening individuals from clumps of other mussels in order to swallow one individual (Nehls 1995). Nehls (1995) presents data on the time taken by eiders to handle such mussels. Across all the observed values, the weighted mean handling time per mussel was 11.8 seconds (n=2,244), yielding a potential maximum intake rate when prey are superabundant of 5.09 mussels min^{-1}. These data refer to mussels with a mean length of 40mm or more. Figure 5.6 of Nehls (1995) indicates that for loose mussels on a tray ie unattached to one another, handling time increases with mussel length and is roughly double for a 40mm mussel as for a 20mm mussel. Assuming that the handling time for natural small mussels that are clumped and attached to one another is also half that of the larger mussels ie 0.5 * 11.8 seconds yields an estimated handling time of 5.9 seconds for small mussels ie an asymptotic intake rate of 10.2 mussels min^{-1}. These values are far lower than that assumed in the model of Kaiser and others (2005) (31.2 bivalves min^{-1}) and reflect the need for eiders to spend time separating mussels from one another rather than simply picking up and swallowing single Macoma. These values are however, also much higher than the calculated intake rate values given by Nehls (1995) ie 1 – 1.65 mussels min^{-1}. However, these latter values are worked out including searching time per mussel whereas the asymptotic intake rate

is assumed to occur when prey are super-abundant, there is no searching time and all the foraging time is spent handling one prey after another. Therefore, the apparently high potential intake rate achieved by eiders feeding on mussels in the model is not a problem. The true test of the values used in the model comes from the comparison between Nehls's (1995) values of observed mussel intake rates in the field and that predicted by the model, given the gradient of the functional response and the prey densities actually present in the model patches (see section 5. 2).

Nehls (1995) does not present any information on the gradient of eiders' functional response. Thus, we have had to revert to the information provided by Richman & Lovvorn (2003) which, having searched through c 200 papers and reports, remains the only source of quantitative information concerning the functional responses of a benthic bivalve feeding duck. We assume that the gradient of the functional response of eiders feeding on either large or small mussels, by virtue of them being on the surface, equates to the steepest value reported by Richman & Lovvorn (2003) ie that for large, shallowly buried prey. In the case of small and large cockles we have used the coefficients provided by Richman & Lovvorn (2003) for scoters feeding on shallowly buried small and large Macoma. In the case of *Ensis*, we have used the asymptote of the function provided by Richman & Lovvorn (2003) for scoters feeding on large deeply buried prey. However, in spite of their length, *Ensis* have a relatively small cross sectional area because of their vertical orientation in the sediment. Thus, we have assumed that the gradient for the functional response of scoters feeding on small, deeply buried prey applies to *Ensis*. The resultant five functional responses used for eiders consuming different diets in the model are presented in Figure 3.8.

The relatively high asymptotic values for the two cockle functional responses suggest handling times of between 1.3 and 2 seconds for cockles. These are not unrealistic given Nehls's (1995) observations that captive eiders can grab and swallow loose mussels in times between 0.5 and 4 seconds. The relatively low asymptotic values for the two mussel functional responses arise because of the need of eiders foraging on real mussel beds to loosen individual mussels from clumps, this being the most time consuming component of consuming mussels in the wild (Nehls 1995).

To derive the intake rate achieved by an eider per second spent actively foraging ie averaged over the course of a foraging bout, the value of the instantaneous intake rate achieved per second spent 'on-bottom' was multiplied by the proportion of each dive cycle that was spent on the bottom (see section 3.7.3.). This average value was then multiplied by the foraging efficiency of the individual in question to generate variation in the intake rates achieved by the birds. This value was then multiplied by zero if the patch was exposed to prevent eiders feeding on exposed patches.

Maximum rate of consuming each diet In many circumstances the rate at which a bird can find food resources does not limit the rate at which it can assimilate energy. Often, constraints on the rate at which the digestive tract can process food and the physical capacity (ie volume) of the digestive tract can limit the rate of energy assimilation. Guillemette (1998) noted that the ingestion rate of shells by common eider is approximately twice as high as the defecation rate and concluded that energy assimilation is constrained by digestion in this species. De Leeuw (1997) noted that the rate of food processing by scaup *Aythya marila* is apparently the

factor that limits crude intake rate over a period of several hours. This problem is particularly true in animals which, like diving ducks, ingest food which has a considerable indigestible component eg the shells of bivalves. The general problem for these birds is thus not to find food (fast enough) but to locate prey with sufficient energy density to fulfil the daily requirement (Bustnes 1998).

Swennen (1976) found that the total mass of shell material in the gut of a single eider with a digestive tract completely filled with cockles was 143g. For one swallowed cockle about half the weight is water and slightly less than half is shell (the rest comprising salt and flesh) (Swennen 1976), so doubling the value of 143g yields an approximate estimate of the total fresh mass gut capacity of c286g. Swennen (1976) found that the average rate at which indigestible material passes through an eider's gut is very nearly one hour (63 minutes). Thus, these birds can process only one gutful of food in an hour. Therefore, we have retained the value of 286g fresh mass h^{-1} as being the maximum crude intake rate achievable by eiders in this model.

Swennen, Leopold & de Bruijn (1989) found that oystercatchers could maintain an intake rate of 1.8 – 2.2mg ash free dry mass sec^{-1} or 540 – 660 mg AFDM per 5 minute period over a two hour exposure period. Taking the maximum of these values and dividing by the mean proportion of bivalve wet flesh mass that comprised AFDM across all the resources exploited by oystercatchers in the model yields an estimate of the maximum intake rate achievable by oystercatchers of 64 g fresh mass h^{-1}.

To determine the maximum rate at which bivalves could be consumed by an eider consuming a given diet in a given patch at a given point in time, the sum of the weighted averages of the dry flesh mass, water mass and shell mass across all resources within that diet was calculated. The maximum crude intake rate of fresh mass per hour constraint value (286g fresh mass h^{-1}) was divided by this value to yield the constraint to eiders' hourly rate of prey item consumption. To determine the maximum rate at which bivalves could be consumed by an oystercatcher consuming a given diet in a given patch at a given point in time, the sum of the weighted averages of the dry flesh mass and water mass across all resources within that diet was calculated. The maximum crude intake rate of fresh flesh mass per hour constraint value (64 g fresh mass h^{-1}) was divided by this value to yield the constraint to oystercatchers' hourly rate of prey item consumption.

Efficiency of assimilating each resource component from each diet As in previous modelling exercises (Stillman and others 2005b), the energy density of shellfish flesh was taken to be 22kJ $gAFDM^{-1}$ while the energy density of a bird's body energy reserves was taken to be 33.4kJ g^{-1}. The basic efficiency with which birds digest shellfish flesh is taken to be 0.85 (Kersten & Visser 1996). As in the models of de Leeuw (1997), Stillman and others (2000a) and Kaiser and others (2005) the efficiency with which birds store energy that they have assimilated was taken to be 0.88 (Kersten & Piersma 1987). Using these numbers alone, each gram of ash free dry mass ingested by oystercatchers was assimilated and converted to body mass reserves.

With the exception of the basic assimilation efficiency, precisely the same values were used in converting each gram of ash free dry mass ingested by eiders to body mass reserves. In the case of eider ducks, calculation of the basic assimilation of energy was somewhat more complicated, primarily by the need to include the cost of crushing the shells. Nehls (1995) found that the proportion of ingested energy that was expended in crushing the shells of whole mussels (over and above that lost in digesting the flesh itself) increased linearly with mussel length. Beadman and others (2003) found that the compressive strength of mussel shells also increased with mussel length and that this trend was far more pronounced in mussels from mid-intertidal shore levels in comparison with those from subtidal areas. We have assumed (on the basis of their very high flesh content) that the mussels studied by Nehls (1995) equate to lay mussels and hence that the equation that he presented to describe the proportion of ingested energy that is expended crushing mussel shells applies to eiders consuming lay mussels in the model. To calculate the proportion of the energy content of mussels from mid-intertidal beds that eiders would need to use to crush them we went through a number of steps. First, we used the AFDM v length relationship for lay mussels to work out the AFDM content of different sized lay mussels. These figures were then multiplied by 22kJ $gAFDM^{-1}$ to yield the total energy content of those mussels. These values were then multiplied by the proportion of that total energy content used to crush shells of a given length (estimated by Nehls 1995) to yield an estimate of the actual energy (kJ) expended in crushing lay mussels of varying length. These numbers were then multiplied by the ratio of the compressive strengths of mid-shore v subtidal mussels (Beadman and others 2003) to yield an estimate of the energetic cost (kJ) of crushing mid-shore mussels of varying length. These values were then divided by the estimated energy content of different sized mid-shore mussels (again derived from an appropriate AFDM v length relationship) to yield the length specific proportion of ingested energy needed to crush the shells of mid-shore mussels. The equation fitted to these values was used to apply to eiders consuming mussels from regulated beds in The Wash. The two equations used in the model are depicted in Figure 3.9.

The equation derived from mid-shore mussels was assumed to apply to eiders feeding on cockles whereas the equation derived from lay mussels was assumed to apply to eiders eating *Ensis*. Thus, the model assumes that eiders, like oystercatchers utilise 15 per cent of the ingested energy in digesting the flesh itself. On top of this, the birds are assumed to utilise a certain proportion of the energy ingested on crushing the whole shells of their prey, this being dependent upon the size and type of prey being consumed. At low ambient temperatures, however, these additive costs are approximately halved due to the fact that some of the heat generated by crushing the shells offsets the increased thermoregulatory demands of the birds. Thus, as in the model of de Leeuw (1997) we assume that the energy costs of shell crushing are halved when temperatures drop below the birds' lower critical temperature.

Rate of metabolising each component The energy expenditure of eider ducks is calculated in the same way as in the model developed and described in detail by Kaiser and others (2005) and is based on the work of de Leeuw (1997). In essence the model ascribes a resting metabolic rate (RMR) to the bird which is constant when the ambient water temperature exceeds the bird's lower critical temperature (LCT) but increases steadily as the temperature falls below this point. The birds incur this RMR all the time whether feeding or resting. On top of this RMR, birds that are actively foraging incur an additional excess diving cost (EDC) dependent upon the amount of time that they spend underwater. This EDC is expressed as a multiple of the RMR. This EDC to RMR ratio also increases with decreasing temperature (De Leeuw 1997) ie diving becomes progressively more costly as the temperature of the water

drops. In the current model the value of RMR which underpins these calculations is derived from direct physiological measurements made on winter-acclimatized captive eider ducks by Jenssen, Ekker & Bech (1989). When floating quietly on the water at temperatures of between 16 and 25^{o}C, the lowest heat production by eiders was 3.83 W. kg^{-1}. At water temperatures between 15^{o}C and 0^{o}C the heat production increased as described by the equation:

$$H\ (W.\ kg^{-1}) = 5.48 - 0.09 * T_w$$

where T_w is the ambient water temperature (Jenssen, Ekker & Bech 1989). We have used these values/equation in the model, assuming an average body mass of 2.174kg (Section 3.7.5). The overall metabolic costs while diving actively involved the summation of the maintenance metabolic costs (RMR) over a period of feeding time plus the extra diving costs (EDC) incurred during the proportion of that feeding time which was spent underwater (given that even when actively feeding only a fraction of a diving bout is spent underwater).

Feeding birds also ingest food at ambient temperatures well below their core body temperature and are required to compensate for the cooling effect of the cold food mass passing through the body (de Leeuw 1997). The cost of doing this was calculated in the same way as de Leeuw (1997) and described by Kaiser and others (2005) with the difference that core body temperature of eiders was set to be 40.4 ^{o}C (Jenssen, Ekker & Bech 1989) and that in this model there was no need to approximate the mass of water ingested with each prey item as water was explicitly modelled as a resource component in the current model. One final factor in calculating the overall rate of energy expenditure by foraging eiders was the additional cost incurred due to the ingestion of salt. Nehls (1995) found that the metabolic rate of eiders increased in response to salt intake. Nehls (1995) estimated that the overall costs of salt turnover were about 1.5 kJ g^{-1} NaCl ingested. We have used this value in the model, coupled with the estimated salt mass content of prey of different sizes (Table 3.1) to calculate the additional cost of salt turnover that foraging birds have to meet. Thus, the total rate of metabolism while an eider was feeding actively comprised the sum of four components: i) the resting metabolic rate * the duration of the feeding period, ii) the extra costs of diving over and above resting costs * the time spent underwater, iii) the costs of heating up each gram of food ingested * the fresh mass of food consumed and iv) the costs of processing the salt mass ingested.

As in previous modelling exercises (Stillman and others 2005b), the basic rate of metabolism of oystercatchers at ambient air temperatures above their lower critical temperature (10^{o}C) was set at 2.5* Basal Metabolic Rate ie 757kJ day^{-1}. This is an average field metabolic rate and therefore incorporates the various sources of energy expenditure incurred by a bird in reality. The thermostatic costs below LCT were calculated using the relationship between published values (Kersten & Piersma 1987) and wader species' body mass. Unlike the case of eiders where the act of foraging by diving into cold water is considerably more energetically expensive then that of resting on the water surface, oystercatcher's rate of metabolism was, as in previous models of this species (Stillman and others 2005b) assumed to be the same whether feeding or not.

3.7.5 Body reserves

The literature review yielded a number of estimates of the body mass of adult eiders in winter. The mean of those values across the sexes was 2,174g. The studies of Gorman & Milne (1971), Milne (1976) and Guillemette (2001) all indicate that there is no change in body mass between the autumn and early spring. The only evidence for pronounced mass changes is amongst female eiders on their breeding grounds immediately prior to the onset of breeding (Guillemette 2001). As this is not relevant in the case of eiders on The Wash, we assume that eiders in the model attempt to maintain a constant overwinter target mass of 2,174g between the beginning of September and the end of March. Camphuysen and others (2002) reported that the mean mass of adult eiders that had died in the winter in the Wadden Sea was 1,476g. This results in a weight at death that is 698g or 32 per cent below the mean winter target mass. This agrees well with the findings of Cabanac (2003) who found mass losses equivalent to between 21 per cent and 39 per cent in starving eiders in winter. Thus, we assume that the mass at which eiders would starve in the model is 1,476g and that they begin the winter with a reserve of 698g and hence a total mass of 2,174g which they seek to maintain throughout the winter.

As in previous models (Stillman and others 2005b), the mass at which oystercatchers would starve was set at 350g and their initial mass was set at 486g ie they start with a body energy reserve of 136g of fat. In the light of empirical data (Stillman and others 2005b), the target body mass of oystercatchers was assumed to increase steadily over the course of the winter by 0.72g day^{-1} to reach a final value of 638g at the end of March.

Only one source of mortality was included in the model ie starvation. A bird was assumed to have died if it failed to maintain any fat reserves ie body mass <= starvation mass. It should be borne in mind, however, that in reality, birds whose body mass is declining may opt to leave a site rather than remain and starve. Thus, what the model predicts is whether each individual can be supported throughout the winter in favourable body condition or not. On the basis of the status of each individual, the model then predicts the proportion of the population that the site can or cannot support under any given set of circumstances. Predictions of the proportion of the population that cannot be supported do not necessarily equate to the proportion of the population that will actually starve.

3.7.6 Fitness & survival

Foragers are assumed to be able to assess fitness measures associated with consuming different diets on their current patch eg small or large mussels. Other patches fall into one of three different categories. (1) Foragers may know the location of a different patch and be able to assess fitness measures on the patch. They can assess the survival consequences of moving to this patch consuming any diet, and know the values of all of the patch's state variables during the current time step. (2) Foragers may know the location of a patch, but not be able to assess the fitness measures associated with different diets. They cannot assess the survival consequences of consuming different diets, and are unaware of any of the patch's state variables. However, they do have an expected fitness measure on this patch, which is used to compare this patch with others. (3) Patches may be of unknown location, and so cannot be considered as potential locations to move to.

The model assumes that eiders can know the location of and can assess the fitness measures and hence the survival consequences of moving to all patches throughout The Wash (category 1 above). This assumes that the birds have perfect knowledge of the suitability of feeding on any patch in The Wash at any point in time.

Given the known distribution of oystercatcher roosts around the periphery of The Wash, the model ascribes each individual oystercatcher to 'belong' to one of these roosting sites (section 3.7.2). The model assumes that oystercatchers which are doing well (ie have a body mass in excess of 75 per cent of their target mass) can know the location of and can assess the fitness measures and hence the survival consequences of moving to all patches within the same region of The Wash eg south(west), south(east) or east (category 1 above). They cannot assess the survival consequences of consuming different diets on any of the other patches outside their 'home' region (category 2 above), and are unaware of any of the patch's state variables. However, they do have an expected fitness measure on these patches which is set to zero. This assumes that the birds which are doing well on their local patches have perfect knowledge only of the suitability of feeding on those patches within close proximity to their roost site. However, the model recognises the likelihood that birds which are failing to do well will look for alternatives within The Wash rather than leaving The Wash altogether or starving without attempting to try to forage somewhere else first. Thus, the model assumes that once an oystercatcher's mass falls below 75 per cent of its target mass it can then know the location of and can assess the fitness measures and hence the survival consequences of moving to all patches throughout The Wash (category 1 above).

The model assumes that there is one component to the fitness of both eiders and oystercatchers. This relates to the fact that a bird's biological fitness must depend in some way on its physical body condition.

The fitness rule assumes that both eiders and oystercatchers will only forage within a time step if, on at least one patch that is available to them, their potential net rate of energy gain equals or exceeds their average net rate of energy gain over the preceding 24 hours. If this condition is not met on any patch, eiders are assumed to roost where they are while oystercatchers are assumed to go to their high tide roost sites on the shores of The Wash. These assumptions are based on the observations of Hart & Brown (2006) that eiders tend to aggregate into rafts at high water close to their feeding grounds whereas oystercatchers roost at various locations around the margins of The Wash (Durell & Atkinson 2004).This rule serves to ensure that birds do not feed at times and in places where the net energy return will be lower than they have experienced in the recent past and will instead concentrate their feeding activity in the best places at the most suitable times. As environmental conditions on the best patches deteriorate (eg due to depletion) and the average net energy gain of birds' drop, the potential net rate of energy gain achievable at more and more places and times will equal or exceed this average value, and birds' feeding activity will spread out in space and time. The model assumes that amongst those patches that meet the criteria at any point in time, each bird will feed in the best available place ie that which maximises the net rate of energy gain during the time step in question. In the light of empirical evidence on the ability of oystercatchers to discriminate between the intake rates that they achieve in different places, each bird's estimation of the net energy gain on each patch is subject to an error of +/- 3 per cent (as in previous models – Stillman and others 2005b). This means that birds will not

necessarily always forage in the patch that yields the absolutely greatest net energy gain but in any patch that yields a net energy gain within approximately 3 per cent of this value.

The consequences of birds' patch choice decisions are determined by the true probability of survival in the chosen location. Given that starvation is the only source of mortality considered in this model, the survival probability is dependent upon the bird's body mass. If a bird's body mass exceeds the starvation mass at the end of a time step the survival probability is set to one, otherwise it is set to zero because the bird would starve. Birds' probability of survival in a location at a given point in time depends solely on whether or not they will starve there during that time step or not.

4. Model simulations

4.1 Model validation simulations

Prior to conducting any of the novel scenario simulations (see below) it was necessary to construct and parameterise the model MORPH. Having done so, it was then necessary to run the model under 'baseline' conditions and establish whether or not it was behaving realistically by comparing the model's outputs with independent empirical data derived primarily from the literature concerning the foraging behaviour and mortality of eider ducks and oystercatchers.

To conduct this validation exercise, the model MORPH was parameterised to simulate the current environment as experienced by the birds in The Wash today (ie the winter of 2005-2006). For the purposes of validation, the model was run using the default values for all the various parameters, in particular the quantities of shellfish resources available on each of the patches in the model. Five replicate simulations were conducted of this baseline scenario to yield the average model outputs. These were then compared with independent empirical datasets (see section 5).

In the initial validation simulations, the harvesting of shellfish, in particular the removal of the bulk of the mussel stock from the Roger lay, most of the Toft lay and part of the Scotsman's sled lay in a six week period in late winter, was included in the model to represent the situation in The Wash in the winter of 2005-2006. Natural England authorised a small harvestable fishery of 782 tonnes of mussel in December 2005 and several small cockle handwork fisheries from July 2005 to February 2006 amounting to 440tonnes. However, ESFJC officer Ron Jessop stated that there was in fact no significant fishery on either the cockle beds or the regulated mussel beds of The Wash in the winter of 2005-2006 and so no stocks were removed from these patches in the model. Comparison of the results of these initial simulations with others in which this late-winter lay fishery was not included produced no significant difference to any of the key model validation tests. This probably reflects the fact that this fishery started late in the winter after the peak in the populations of both eiders and oystercatchers had occurred, and finished only a few weeks before the end of the modelled period. For simplicity, in establishing a baseline scenario against which the results of the scenarios described in the following section could be compared, it was decided to run the actual model validation runs in the absence of shellfish harvesting and not to include this factor in the novel scenarios either. Given the changes to the scale of the lay fishery and its management and the changes to the stocks of other shellfish explored in these novel scenarios it seemed inappropriate to attempt to predict what the magnitude of harvesting of any of these resources might be under any given novel scenario. Rather, it was decided that in order to clarify the role of the magnitude of the autumn shellfish stocks on the birds' well-being it would be simpler to ignore shellfish harvesting as an issue in this modelling exercise.

4.2 Novel scenarios

The series of simulations which are described in this section evolved over the course of the project as a result of discussions between CEH, Natural England and the Eastern Sea

Fisheries Joint Committee. The final set of simulations was agreed with Natural England in February 2007 following a meeting with ESFJC on the 31st of January 2007.

In summary, the **principal aim** of the model simulations of novel scenarios was to assess the impact on eider and oystercatcher survival of varying the magnitude of the commercially cultivated mussel stock (in terms of the number of lays and stocking density) against a number of likely alternative wild shellfish stock levels (ie mussels, cockles and other shellfish in particular *Ensis*). A **secondary aim** was to assess the way in which the distribution of predation pressure exerted by both eiders and oystercatchers across the various patches of resources changed in response to variation in the magnitude of the commercially cultivated mussel stock (again in terms of numbers of lays, stocking densities) against a number of likely alternative wild shellfish stock levels. The simulations are summarised below and further detail provided in the following sections.

Series 1: investigate impact on eider and oystercatcher survival and predation rates on shellfish resources of gradually reducing the area of the lay fishery while maintaining the mussel numerical density on individual beds. Set against varying background shellfish levels (wild mussel, cockle, *Ensis*)

Series 2: investigate impact on eider and oystercatcher survival and predation rates on shellfish resources of varying the mussel density on individual lays, the lay area and shore height of lays (scenarios: doubling of lay area & halving of mussel density; halving of lay area and doubling of mussel density; equalised mussel density; equalised lay area, mussel density, and shore height). Again set against varying background shellfish levels (wild mussel, cockle, *Ensis*)

Series 3: investigate maximum peak population size of eider that can be maintained with an acceptable level of mortality (ie average overwinter mortality in a healthy system) when wild mussel and cockle stocks healthy but razor clam and cultivated mussel stocks varied.

4.2.1 Series 1 Simulations

This was the series of simulations that was used to address the principal aim of the modelling study. The strategy that was employed in this series was to vary the total stock of mussels on the several lays in a series of steps by reducing lay area / number but maintaining mussel density, and to explore the implications of doing so for the proportion of the current population of eiders and oystercatchers that can be supported throughout the winter. This was repeated against a number of different 'background' resource levels (ie regulated mussels, cockles and other shellfish in particular *Ensis*) to explore whether the implications of varying the lay fishery on the birds varied depending upon the abundance of alternative shellfish resources. These alternative background stock levels were set on the basis of experience of how the stocks of these shellfish have varied in the past, and might realistically be expected to do in the future.

Varying the several lay mussel fishery Under the baseline conditions the commercially cultivated mussel lays in the model were represented by six lays (Roger, Toft, Clay Hole, Scotsman's Sled, Herring Hill and Black Buoy). The area and stock density of mussels on each lay were derived from the surveys of the lays conducted by ESFJC in autumn 2005 (see section 3.4). Reductions in the size of the commercially cultivated mussel stock were simulated by gradual reductions in the areas of these lays. At present, approximately 90 per cent of the total stock of lay mussels (10,336 tonnes in the model cf 10,000 – 15,000 tonnes estimated by ESFJC) occurs on the two principal lays ie Roger and Toft. Thus, the first five steps in the sequence of reducing the lay fishery were achieved by the gradual reduction of the areas of these two principal lays (Table 4.1). Subsequent steps were achieved by the further removal of the smaller lays in turn until all lays had been removed (Table 4.1). These steps resulted in a gradual stepwise reduction in the total stock of lay mussels available to the birds at the start of the winter.

Table 4.1 Sequence of reduction in the total stock of lay mussels achieved by the gradual reduction of the area of lays available to the birds.

Step Number	Variation to Mussel Lay areas	Total stock of mussels on all lays (tonnes)	% of existing lay stock
	Default areas for all lays	10,336	100
1	Area of Roger * 0.65	8,267	80
2	Area of Roger * 0.30	6,200	60
3	Roger lay removed	4,384	42.4
4	No Roger, area of Toft * 0.33	2,067	20
5	Roger and Toft lays removed	950	9.2
6	Roger, Toft, & Clay Hole removed	516	5
7	Roger, Toft, Clay Hole & Scotsman's sled removed	107	1
8	All lays removed	0	0

Additional simulations, the results of which are not presented here, revealed that the results of varying the total stock of lay mussels in the way described here did not produce markedly different results to those produced by an alternative way of achieving the same gradual reduction in the total stock of lay mussels. This alternative, which was explored initially, reduced the total stock of lay mussels in steps by applying a fixed proportionate decrease in the numerical density of mussels across all the lays simultaneously. It was anticipated that this might produce different results due to the fact that reducing the density of mussels has the potential to directly and immediately reduce the intake rate that eiders can achieve in the model (via their functional response) whereas reducing the areas of the lays will only do so over a longer time scale if intensified depletion of the remaining stocks lowers the numerical density of the mussels sufficiently. However, although the predicted proportion of the current eider population that could not be supported at a given lay stock level differed slightly between the two alternatives, the overall pattern and magnitude of the reduction in the proportion of the current eider population that could be supported was the same under the two alternative methods of reducing the stock level. Thus, only the series in which we have altered the areas of the lays are explored in detail here. It can also be considered that in terms of how the several lay fishery might contract in the future (if this were to occur), it would be more

likely that individual lay holders would reduce the extent of their holdings rather than reduce the density at which they grow their mussels. A small-scale fishery in the future would likely consist of fewer, smaller but well-stocked lays rather than six lays of the existing size stocked at low densities. Thus, the current series of simulations is probably a more realistic representation of possible future lay management scenarios.

Varying the background shellfish resource level The total stocks of the shellfish resources in the model under the present circumstances are based on the results of the surveys of the areas, numerical densities and size frequency distributions of shellfish on the regulated mussel beds (ESFJC autumn 2005), cockle beds (Ecomaris Ltd. June 2005 and ESFJC autumn 2005 (and spring 2006 where necessary)) and *Ensis* beds (CEFAS). This information is combined in the model with the estimated component masses of bivalves of each size class of each species to yield the total tonnage of live shellfish mass on each patch and hence across The Wash as a whole. This complicated process yielded estimates of the three non-lay shellfish resources of 10,047t of regulated mussels, 41,016t of cockles (34,448t excluding the Heacham bed) and 10,835t of *Ensis*.

ESFJC (2005) estimated a stock of 13,419t of mussels on the regulated mussel beds in autumn 2005 and 14,643t of cockles in spring 2005 (Jessop & Graves 2005). ESFJC resurveyed six of the principal cockle beds in autumn 2005. Across these six beds there was a marked increase in the tonnage of cockles of fishable size and a less pronounced increase in the tonnage of juvenile cockles. Applying the resultant spring-autumn multiplication factor for fishable and juvenile cockles to the total stock of fishable and juvenile cockles across all cockle beds surveyed in spring 2005 (4,488t and 10,155t respectively (Jessop & Graves 2005)) yielded an estimated stock of 19,276t of fishable cockles and 17,954t of juvenile cockles in autumn 2005 ie a total stock of 37,230t. This then compares with the value of 34,448t generated in the model for the same set of patches (ie excluding the Heacham bed). Ron Jessop of ESFJC has commented that the spring 2005 to autumn 2005 increase in the stock of cockles, particularly that of fishable cockles, which has been used here to derive an independent estimate of the autumn 2005 stocks for comparison with the stock used in the model, was atypical and reflected the growth of the strong 2004 year class over the summer of 2005. Many of these grew from being juvenile to being part of the fishable stock. Be that as it may, the comparable value in the model of 34,448t resulted from the actual survey data from the six beds surveyed in autumn 2005 and, for those beds not surveyed then, from back-calculated values of the autumn 2005 stock based on the spring 2006 survey of those beds coupled with the over-winter change in numerical densities between autumn 2005 and spring 2006 on those beds surveyed on both occasions. In other words the estimated stock of cockles in the model is not solely dependent upon the atypically strong growth of the 2004 year class between spring 2005 and autumn 2005. Dave Palmer of CEFAS viewed an estimated stock of 10,835t of *Ensis* as being realistic. Thus, the stocks of the three principal, alternative, non-lay shellfish resources used in the model to mimic current circumstances, accord reasonably well with current knowledge of autumn shellfish stocks.

Shellfish stocks in The Wash are highly variable and it is for this reason that we have conducted a range of scenarios against which the scale of the lay fishery was varied (Table 4.2). Peak stocks of mussels on the regulated beds appear to be declining: 30,000 tonnes was recorded in 1920's, 25,000 tonnes in 1940's, 18,000 tonnes in 1981 (Dare and others 2004) and c 13,000 tonnes today. However, stocks of mussels on the regulated beds reached

historically low values of c 2,500t between 1992 and 1998 (Stillman and others 2003). Thus, we have taken a value of 2,500t to represent a 'low' regulated mussel stock, today's value of c 13,000t to represent a 'medium' value and 20,000t to approximate what would today be considered a 'high' stock of mussels on the regulated beds. Cockle stocks in The Wash are also very variable from year to year (Dare and others 2004). In the years 1992, and 1995-1998, the mean cockle stock in The Wash was very low and had a mean value of around 4,000t (Stillman and others 2003). We have taken this to be the 'very low' value in our model. In the years 1993 and 1994 the mean cockle stock in The Wash was 15,000t (Stillman and others 2003) and we have taken this to represent a 'low' cockle stock. Cockle stocks are currently recovering from these low values and we have classified the current stock as being 'medium'. There was an historically high cockle stock of at least 60,000 tonnes of fishable cockles in the late 1960s (Dare and others 2004). However, it is unlikely that such an abundant stock will be seen again in the near future. So, in consultation with ESFJC, we have taken 50,000t of cockles (including both fishable and juvenile cockles) to represent what would be considered to be a 'high' autumn cockle stock in the present day or near future. *Ensis directus* is a non-native shellfish species that was first identified in European waters in the German Bight in 1979 (Palmer 2003). It is now widely distributed around The Wash, occurring on subtidal banks, and is estimated to have a total stock of c 10,000t. However, this species appears to recruit only intermittently and to die when it reaches an age of c seven years. These characteristics result in the occurrence of marked oscillations in the stock of *Ensis* and we have assumed a 'low' stock level to be about 10 per cent of this peak value ie c 1,000t.

Using various combinations of these alternative shellfish stocks we created five different scenarios against which we varied the scale of the several lay fishery (Table 4.2). These alternative scenarios are taken to represent possible future combinations of shellfish stocks in The Wash based on the premise that what has happened before, may happen again.

Table 4.2 Values for the total stocks of the alternative shellfish resources used to create five alternative scenarios against which the scale of the several lay fishery is altered.

Scenario	Shellfish resource (tonnes)			Description of shellfish stock levels
	Regulated mussels	Cockles	*Ensis*	
Scenario 1	10,047	41,016	10,835	Both regulated mussels and cockles 'medium', *Ensis* 'high'
Scenario 2	2,500	15,000	10,835	Regulated mussels 'low', cockles 'low', *Ensis* 'high'.
Scenario 3	2,500	4,000	10,835	Regulated mussels 'low', cockles ' very low', and *Ensis* 'high'
Scenario 4	10,047	41,016	1,083	Regulated mussels and cockles 'medium', *Ensis* 'low' (ie *Ensis* directus absent though still a low stock of native razor fish).
Scenario 5	20,000	50,000	1,083	Both regulated mussels and cockles 'high', but *Ensis* 'low' (ie *Ensis* directus absent though still a low stock of native razor fish).

In all cases, manipulations to the total tonnage of shellfish available were made by altering the initial numerical density of the shellfish rather than by altering the areas of the shellfish beds. Conducting the manipulation in this way means that the changed shellfish stocks will influence the intake rates achieved by both eiders and oystercatchers by virtue of altering the starting position for prey density in the functional responses (Figure 3.8). Manipulating the shellfish stocks by altering bed areas would have had a more pronounced effect on oystercatchers but less of an effect on eiders by virtue of the relative strengths of interference assumed in the two species. Thus, the method of manipulation that we have deployed results in insights into how both species might be affected rather than just oystercatchers.

It must be emphasised that the values for the total tonnage of stocks used in the model to define 'high', 'medium' and 'low' stocks refer to autumn rather than spring stocks. The former are probably usually greater than the latter (due to overwinter depletion by birds, mortality due to other factors and loss of condition at the level of the individual bivalve). This needs to be borne in mind in interpreting the results of these simulations and in predicting, on the basis of the model's results, what the likely implications for eider and oystercatcher populations might be of future shellfish stocks when these are routinely surveyed in spring rather than autumn.

4.2.2 Series 2 simulations

In this series of simulations the aim was to explore the consequences both for the birds, and for the predation pressure that they exert on the mussel lays, of gross changes to the way in which the commercially cultivated mussel lays are managed. To this end, we conducted scenarios in which we retained the same total stock of lay mussels as at present ie 10,336t but altered one key aspect of the way in which this resource could be distributed by the commercial fishermen ie the area over which a given stock is laid. Within the constraints imposed by the extent of the several order and the problems of density-dependent mussel mortality, commercial fisherman have the ability to alter the density at which they lay mussels (individuals m^{-2}). Thus we explored scenarios in which the area of all six principal lays was halved but the numerical density of mussels on each was doubled. In contrast we also explored a scenario in which the area of all six principal lays was doubled but the numerical density of mussels on each was halved. In two further scenarios we first equalised the numerical density of mussels across all six principal lays and then also equalised the area and shore level of the six lays in order to make them all identical in every regard (except location). These scenarios are summarised in Table 4.3. The principal purpose of these scenarios was to examine the extent to which the proportion of eider and oystercatchers that can be supported is affected by the extent to which lay mussels are aggregated into one or a few hotspots as opposed to being more evenly distributed. Of equal interest, is whether varying the management of the lay fishery in these ways has any influence on the distribution of foraging birds between the lays and alternative resources and hence the overall level of predation pressure exerted by the mussel-eating birds on the lay fishery.

Table 4.3 Description of the manipulations to the management of the six principal commercially cultivated lays under each of five alternative scenarios.

scenario	Total stock of mussels on all lays (tonnes)	% of existing lay stock	Description of manipulation of lay management
Baseline	10,336	100	Default bed areas and numerical densities
Scenario 2a	10,336	100	All lay areas halved but stock densities doubled
Scenario 2b	10,336	100	All lay areas doubled but stock densities halved
Scenario 2c	10,336	100	Stocking density equalised across all lays
Scenario 2d	10,336	100	All lays identical in terms of stock density, area and shore level

At the suggestion of ESFJC it was decided to conduct these scenarios not just against the background of alternative shellfish resources present today (ie cockle and regulated mussel stocks 'medium' and *Ensis* 'high' (Table 4.2 scenario 1), but to do so against a background in which the stock of *Ensis directus* was assumed to have crashed again to c 1,000t. This was to establish whether the magnitude of any apparent effect of changes to the lay management on the predation pressure exerted by the birds was dependent upon the availability or otherwise of a healthy stock of *Ensis*, this being highly unpredictable on a year to year basis.

4.2.3 Series 3 simulations

In all of the preceding series of simulations we held the peak population of eiders constant at 3,000 birds. The principal results of these simulations were predictions of the change in the proportion of the existing eider and oystercatcher populations that could be supported under the alternative scenarios. What these simulations do not indicate is the maximum size of the population that could be supported under alternative shellfish scenarios without the proportion of birds failing to be supported increasing too much ie to get an idea of the 'carrying capacity' of the system. Thus, we conducted a further series of simulations in which we varied the peak population of eider ducks against four alternative background shellfish resource combinations. These simulated situations in which either one or other or both of the commercially cultivated lay mussel stock and the *Ensis* stock was healthy (ie as it is today) or low (ie no commercially cultivated lays or 1,000t of *Ensis*). In all cases these simulations were, as requested by Natural England, conducted assuming a healthy stock of regulated mussels (ie 20,000t) and cockles (ie 50,000t) in order to establish what eider population could be supported when wild, native shellfish stocks in The Wash are healthy but in the presence/absence of 'un-natural' shellfish resources ie commercially cultivated lay mussels and non-native *Ensis directus*.

5. Model validation

5.1 Proportion of time spent feeding

A key test of the model is whether it mimics the amount of time that birds devote to foraging each day in order to survive. It is essential to establish whether model birds have to 'work as hard' to survive as birds do in reality. If this were not the case, then predictions of the consequences of changes to the environment in simulations in which the scale of the lay fishery or background shellfish resource levels are altered may be optimistic due to overly benign baseline conditions. Conversely, if model birds have to forage very much longer than birds do in reality, then predictions of the consequences of changes to the environment may be pessimistic due to overly harsh baseline conditions.

The model predicted that under current conditions, the proportion of daylight hours that eiders spend feeding ie engaged in dive bouts, increases from *c* 0.1 in early autumn to a peak of *c* 0.20 in mid-winter and that this is then maintained throughout the rest of the winter period (Figure 5.1a). The literature review yielded a wide range of observed values for the proportion of time that eiders spend feeding. The minimum value was 0.02 reported by Nehls (1995) as occurring in September. The maximum recorded value was 0.56 reported for eiders in mid-winter (Guillemette 1998). Values from other studies and other times of year produced values between these lower and upper limits (0.46, 0.33 (Guillemette 1998), 0.30, 0.32, 0.35, 0.42 (Guillemette 2001), 0.11, 0.23 (Hilgerloh 1997), and 0.56 (Goudie 1984 cited in Laubhan & Metzner 1999)). The most comprehensive dataset on the way in which the proportion of time spent feeding varies seasonally is that provided by Nehls (1995). Figures 7.7 and 7.14 of Nehls (1995) reveal a gradual increase in the proportion of time spent feeding between September and November and then an approximately constant value of c 0.25 until March. This data is illustrated by the broken solid line in Figure 5.1a. The model output not only falls within the admittedly wide range between the observed upper and lower limits, but also agrees remarkably well with the seasonal pattern found by Nehls (1995). Errors in any of a large number of parameters and functions in the model could have resulted in the model predicting that the birds spend wholly incorrect amounts of time foraging during daylight. It does not do so.

The model predicted that under current conditions, the proportion of daylight hours spent foraging by oystercatchers varies between 0.28 and 0.71, increasing from an initially low value to reach a peak in mid-winter before declining again in late winter and early spring (Figure 5.1b). The values for the likely upper, lower and mean values were derived from a review of oystercatcher feeding behaviour compiled by Zwarts and others (1996a). This review tabulated values for the amount of time spent on the feeding grounds by oystercatchers and the proportion of time that they spent feeding while on the feeding grounds. Multiplying these two values together yielded estimates of the actual amount of time spent actively feeding. Only those records relating to birds feeding in the wild on cockles and mussels in the non-breeding season were extracted from this dataset. The resultant figures (n = 51 excluding three outliers) were then expressed as a proportion of the mean duration of daylight in the model (625 minutes). This yielded a maximum value of 0.65, a mean value of 0.38 and a minimum value of 0.23. These values are depicted in Figure 5.1b. With one exception in mid-

winter, the proportion of time spent feeding during daylight by oystercatchers in the model fell between the lower and upper limits derived from the review of Zwarts and others (1996a). Errors in any of a large number of parameters and functions in the model could have resulted in the model predicting that the birds spend wholly incorrect amounts of time foraging during daylight. It does not do so.

5.2 Daily consumption of food

Nehls (1995) presents values for the 'instantaneous intake rate' achieved by eiders feeding on mussels by head dipping and by diving. These values range between 1.0 and 1.65 mussels min^{-1} or 0.8 and 0.91 g AFDM min^{-1}. The combination of the functional response and the diving sub-model used in the model means that across the full range of possible water depths (0m - 8m) and initial mussel densities (c100 mussels m^{-2} - c2,100 mussels m^{-2}) on the mussel lays, eiders feeding on the large mussel diet could attain intake rates of between 0.48 and 2.30 mussels min^{-1} (mean = 1.55 mussels min^{-1}) or 0.19 – 0.93 g AFDM min^{-1} (mean = 0.63 g AFDM min^{-1}) These potential ranges do however include the intake rates available in many water depth/ mussel density combinations when the birds in the model would not actually choose to forage. At many combinations of water depth and prey density within the model, the intake rate achievable by eiders in the model fell within the ranges reported by Nehls (1995). In particular, the average intake rates achievable by eiders in the most preferred mussel patch in the model (averaged across potential water depths of 0 – 8m and using the initial numerical density of mussels) was 1.8 mussels min^{-1} and 0.7 g AFDM min^{-1}. These values are remarkably close to the independent empirical data reported by Nehls (1995).

The literature review yielded a number of estimates of the daily consumption of food by eiders, expressed in terms of the ash-free dry mass (AFDM) of flesh ingested: 107g (Swennen 1976), 138g (Nehls 1989), 130g – 187g (Nehls 1995), 92g – 138g (Hilgerloh 1997), 130g – 180g (Nehls, Hetzler & Scheiffarth 1997), 178g (Camphuysen and others 2002). Thus, the range of reported values is from 92g – 187g. The model predicts that throughout the modelled period, the average daily consumption of AFDM by eiders fell within this range (Figure 5.2a). Daily consumption was predicted to increase from autumn to mid-winter and to decline slightly thereafter.

The literature review also yielded a number of estimates of the daily consumption of food by oystercatchers, expressed in terms of the ash-free dry mass (AFDM) of flesh ingested. John Goss-Custard calculated (on the basis of oystercatchers' energetic requirements at thermoneutrality, the costs of thermoregulation at temperatures below LCT and the rate of mass gain observed over-winter in the wild) (and assuming certain values for the energy density of the food and the birds' assimilation efficiency)) that the daily AFDM consumption of oystercatchers varied between 38g and 59g AFDM. Beukema (1993) reported values of 40g AFDM between May and October and 55g AFDM between November and April. Kersten & Piersma (1987) measured daily consumption of captive birds held in outdoor aviaries to be 35g AFDM at ambient air temperatures above 10°C and 50g AFDM at sub zero temperatures. Zwarts and others (1996b) reviewed a number of studies of oystercatcher's daily food consumption. The majority of these records (n=38) related to captive birds feeding on mussels and cockles. The range of values was between 24g and 42g with a mean of 32g AFDM d^{-1} and a lower 95 per cent limit of 22g AFDM d^{-1}. Thus, the likely range of values is from 22g to

60g AFDM d^{-1}. The model predicts that throughout the modelled period, the average daily consumption of AFDM by oystercatchers fell within this range (Figure 5.2b). Errors in any of a large number of parameters and functions in the model could have resulted in the model predicting that the birds consumed wholly incorrect quantities of food. It does not do so.

Another way of expressing the daily food intake of birds is in terms of the fresh mass of material that the actually ingest ie wet shellfish flesh in the case of oystercatchers and live mass (including shells) in the case of eiders. The literature review yielded a number of estimates of the daily consumption of food by eiders, expressed in terms of the live mass of whole shellfish ingested. These values are presented in Table 5.1.

Table 5.1 Values for the daily consumption of whole live shellfish by eiders.

Diet	Daily consumption (g live mass)	Source reference
Mussels	2000g	Guillemette, Reed & Himmelman 1996
Mussels	1,781g (in spring)	Guillemette 1998
Mussels	1,906g (in mid-winter)	Guillemette 1998
Mussels	2,098g (in late winter)	Guillemette 1998
Mussels (small)	1,500g	Ross & Furness 2000
Mussels (large)	2,700g	Ross & Furness 2000
Mussels (<25mm)	1,500g	Bustnes & Erikstad 1990
Mussels (>40mm)	2,500g	Bustnes & Erikstad 1990

Thus, the range of reported values is from 1,500g – 2,700g. The model predicts that with the exception of a short period in mid-winter, the average daily consumption of shellfish by eiders falls within this range throughout the modelled period (Figure 5.3a). Daily consumption was predicted to increase markedly from autumn to mid-winter and to decline again thereafter. This decline from winter to spring is consistent with the findings of Guillemette (1998).

Unpublished work by John Goss-Custard has estimated that the daily consumption of fresh flesh mass by oystercatchers varies between 238g and 372g over the period September to March. However, these values are derived directly from the calculated daily consumption of AFDM on the assumption that the AFDM comprises 16 per cent of the wet flesh mass (Zwarts and others 1996a). Within the model, the values of AFDM and water mass used for each size class of mussels on lays and natural beds resulted in an average value of 12.3 per cent. Using this value, we have converted the lower and upper limits for AFDM daily consumption described above ie 22g and 60g to equivalent values expressed in terms of wet flesh mass ie 180g and 478g. The model predicts that throughout the modelled period, the average daily consumption of wet flesh mass by oystercatchers falls within this range (Figure 5.3b). Errors in any of a large number of parameters and functions in the model could have resulted in the model predicting that the birds consumed wholly incorrect quantities of food. It does not do so.

5.3 Daily energy expenditure

Drent & Daan (1980) concluded that the maximum daily work capacity of birds during the breeding season (generally assumed to be the most energy demanding period for most birds) is approximately 4 * BMR. In the vast majority of studies of the daily energy expenditure (DEE) of free-living birds, the calculated DEEs have indeed been below this critical value. However, Nehls (1995) reported that the daily energy expenditure of eiders in winter is 3,022kJ, equivalent to approximately 4.3 * Basal Metabolic Rate of 700kJ day^{-1}. De Leeuw (1997) gives a value of 4.2 * BMR for tufted ducks in winter. De Leeuw (1997) also estimated the DEE of scaup in winter to be 1,063kJ day^{-1}. This is equivalent to approximately 3.8 * BMR. Thus, it would seem that all diving ducks in winter expend energy at a rate that is close to or slightly in excess of the proposed critical threshold of 4 * BMR. De Leeuw (1997) attributed this to the energetically costly mode of foraging employed by diving ducks coupled with the relatively poor nutritional quality of the material that they consume ie whole bivalves. Thus, the likely upper limit to the DEE of eiders is c 3,000 kJ. The lowest possible daily energy expenditure that eiders in the model could have would be achieved if they did not feed at all. In this case they would not incur any additional energetic costs over and above their resting metabolic rate (RMR) due to factors such as diving underwater and heating, crushing and digesting shellfish. The RMR of eider ducks is temperature dependent (below their lower critical temperature (15^{o}C in water (Jenssen, Ekker & Bech 1989)). Across the modelled period eiders' RMR averaged 900kJ day^{-1} ie 1.3 * BMR. The actual average DEE of eiders was consistently above their RMR and below the upper limit (Figure 5.4a). Errors in any of a large number of parameters and functions in the model could have resulted in the model predicting that the birds expended wholly incorrect amounts of energy each day. It does not do so.

In the case of oystercatchers, the rate at which they expend energy when ambient temperatures exceeded their lower critical temperature was, as in previous modelling exercises (Stillman and others 2005b), set at a constant value of 757kJ day^{-1} ie 2.5 * BMR. This is effectively a field metabolic rate which integrates the average proportion of time that birds in the wild spend feeding and not feeding. Thus, in the model this rate was applied independent of whether a bird was feeding or not. Given that the proportion of time spent feeding by oystercatchers in the model was within the likely upper and lower bounds (section 5.1) the use of this value to set the rate of energy expenditure by oystercatchers seems appropriate. The actual DEE of oystercatchers in the model was however, influenced by the ambient temperature and showed an increase from autumn to winter followed by a decline in spring in line with the seasonal change in the air temperature (Figure 5.4b).

5.4 Body mass

The model predicted that the bulk of the eiders in the population were able to maintain their body mass at or very close to the assumed constant overwinter target mass of 2,174g (Figure 5.5a). Only from late January onwards was there evidence of a slight decline in the average body mass of surviving birds. This is probably a consequence of the gradual decline in the body mass of birds that were destined to 'starve' ie not be supported, over a period of time before they reached their starvation mass. It is also possible that this late-winter decline in the average body mass arises as a consequence of some of the more successful individuals that survived the winter also failing to maintain their body mass throughout. Nonetheless, the

model predicts that under current circumstances the average body mass of those birds that do not starve is well in excess of the starvation mass. Under existing circumstances the majority of the population are not in danger of starving. Nonetheless, the fact that a dip in average body mass occurred in late winter, coupled with the predicted proportion of time spent feeding being in line with expectations (section 5.1), indicates that the general ability of eiders to maintain their body mass throughout the modelled period, and the relatively low over-winter mortality in the model (section 5.6), does not reflect an overly benign model world.

The model predicted that the bulk of the oystercatchers in the population were able to increase their body mass in line with the assumed increasing target body mass throughout the modelled period (Figure 5.5b). Between late November and February there was slight evidence of a small proportion of birds being unable to maintain the target rate of mass increase. However, as no oystercatchers were predicted to starve (section 5.6), this was clearly only a temporary problem. By March all birds were predicted to have attained their target mass again. This mid-winter dip in condition may rise from a combination of a number of factors. For example, thermostatic energy demands in mid-winter are higher than at other times of year. Also, the generally less extreme tides in mid-winter may have resulted in less time available for feeding on spring tides as opposed to the equinoxial tides in autumn and spring. The fact that this dip occurred, coupled with the predicted proportion of time spent feeding being in line with expectations, indicates that the general ability of oystercatchers to increase their body mass throughout the modelled period and the lack of over-winter mortality in the model (section 5.6) does not reflect an overly benign model world.

5.5 Distribution

The location of eiders and oystercatchers was recorded on each of five over flights of The Wash conducted between November 2005 and March 2006 (Smith, Hall, Worden, Harrison, Allen, Bradbury, Cranswick, Woodward, Shepherd, Paynter & McGill 2006). Given that the boundaries of each of the shellfish beds in the model were available within a GIS format (ESFJC data) it would have been possible to allocate each observation of either an oystercatcher or eider as falling within one patch of shellfish or another and to test the model's predictions of the birds' distribution at the scale of the individual patch. However, the accuracy of each sighting from the air was in fact only certain to within 200 – 300m (Smith, Hall, Worden, Harrison, Allen, Bradbury, Cranswick, Woodward, Shepherd, Paynter & McGill 2006). Moreover, some of the birds surveyed may not have been feeding at the time of the over flight but roosting near their chosen foraging patch (Hart & Brown 2006). Given these uncertainties about the accuracy with which the over flight data recorded the precise location at which birds were foraging it was decided to broaden the scale at which we tested the model's ability to predict bird distribution to a regional scale. Accordingly we divided The Wash into five arbitrary regions (Figure 5.6). We allocated each observation of a bird/flock of birds in the over flight dataset to one of those regions (Figure 5.6) and then calculated the average proportion of the eider and oystercatcher population counted in each region across the five over flights. We then allocated each of the model patches to its appropriate region and calculated the average proportion of the model population occurring on the patches within each region over the course of the modelled period. Comparisons between this regional scale distribution predicted by the model and that observed during the over flights revealed a very close match in the case of both eiders and oystercatchers (Figure 5.7). Nearly 75 per cent of the eiders in reality and in the model were predicted to occur in Region 2 ie that including the

Roger and Toft lays (Figures 5.6 and 5.7a). Eiders were rarely seen in other regions of The Wash and were not predicted by the model to occur there to any great extent. In contrast to eiders, oystercatchers were observed to be spread much more evenly between the five regions of The Wash (Smith, Hall, Worden, Harrison, Allen, Bradbury, Cranswick, Woodward, Shepherd, Paynter & McGill 2006) (Figure 5.7b) and this was the pattern generated by the model too. It should be pointed out that in the case of oystercatchers this is not a true validation test of the model as the initial distribution of oystercatchers around The Wash used in the model was based on the observed distribution (section 3.7.2). However, in the model, oystercatchers that failed to maintain their target mass were free to move to other regions of The Wash and this could, over the course of the winter, have resulted in the distribution of birds changing markedly from the initial distribution. Clearly this did not happen.

5.6 Over-winter 'mortality'

There is very little hard data on any aspect of the population ecology of sea ducks (Kirby, Evans & Fox 1993). Relatively little is known about winter mortality rates. However, Guillemette, Ydenberg & Himmelman (1992) state that "we have no difficulty imagining that starvation could be a major cause of natural mortality in wintering (common) eiders". Richman & Lovvorn (2003) found that very nearly half of the annual mortality of adult female spectacled eiders *Somateria fischeri* appears to occur in the non-breeding period when the ducks are at sea. They concluded that regardless of the mechanism, a major limitation on the population is adult mortality much of which occurs away from the breeding area.

The limited quantitative information concerning the mortality of eiders that is available in the literature can be summarised as follows. Coulson (1984) reported an annual mortality of female eiders of 10.5 per cent. Krementz, Hines & Caithamer (1996) reported an annual mortality of female eiders of 12.7 per cent. Fleet (2001) reported an overwinter mortality of common eiders of 6 per cent while Piersma & Camphuysen (2001) recorded an exceptionally high overwinter mortality of 15 per cent. On the basis that in spectacled eiders, approximately half of the annual mortality occurs outside the breeding season, one can estimate that the annual mortality figures presented by Coulson (1984) and Krementz, Hines & Caithamer (1996) equate to overwinter mortality rates of 4.83 per cent and 5.8 per cent respectively. These figures in conjunction with those of Fleet (2001) suggest that an overwinter mortality rate of around 4-6 per cent is typical of eider populations and that a value of 15 per cent is exceptional.

The model predicted that under current conditions in The Wash ie a peak population of 3,000 eiders exploiting an abundant stock of lay mussels and also having access to moderate stocks of cockles, mussels on regulated beds and a high *Ensis* stock, the over-winter mortality of eiders is on average 3.9 per cent (range 2.7 per cent to 5.7 per cent across five replicate simulations). Thus, there is very close agreement between the admittedly imprecise estimate of the typical over winter mortality of eiders in reality and that predicted by the model. Errors in any of a large number of parameters and functions in the model could have resulted in the model predicting wholly incorrect over-winter mortality values. It does not do so.

The over-winter mortality experienced by oystercatchers in The Wash is known to vary between years in relation to the abundance of the shellfish stocks (Stillman and others 2003).

Overwinter mortalities in the winters of 1992-1993, 1995-1996 and 1996-1997 when mussel and cockle stocks crashed were between 10 per cent and 26 per cent whereas in the other years in the early-mid 1990s the mortality rate was around one per cent (Stillman and others 2003). The extent of the lay fishery in The Wash in the 1990s was considerably less than today and the stocks of mussels on the regulated beds and of cockles were also less than today (section 4.2.1). Thus, it is not surprising that the model, when parameterised to mimic the present day, predicted no oystercatcher mortality. This could arise due to any number of errors in the model parameterisation or its underlying assumptions such that the model world is far too benign for oystercatchers. However, if this were the case then the dip in mean body mass in mid-winter would not have occurred (section 5.5) and nor would the birds be feeding for a significant proportion of the day (section 5.1) especially in mid-winter. These 'subsidiary' model validation tests give some confidence that the prediction of no oystercatcher mortality under current conditions is not a result of poor parameterisation but that it reflects the abundance of shellfish stocks available to them.

5.7 Conclusions

In summary, five replicate simulations of the model MORPH were conducted in which the current environment of The Wash, as experienced by common eiders and oystercatchers was simulated. The output of these simulations was compared with independent empirical data concerning the: foraging behaviour, food consumption, energy expenditure, body mass, distribution and mortality of eiders and oystercatchers. In general, the model outputs were consistent with these independent data. This provides confidence that the birds in the model behave as do birds in reality and that the key features of the system have been incorporated in the model. On this basis, it is then possible to have some confidence in the predictions of the model when used to simulate novel environmental conditions in which the scale of the several mussel fishery is altered and/or the abundances of alternative shellfish resources are altered.

6. Model results

In all of the results presented in this section it needs to be borne in mind that a bird whose body condition declines to reach the starvation mass need not starve in reality. Mass mortality of eider ducks and oystercatchers due to unfavourable food situations have been recorded in The Wadden Sea and The Wash (Hulscher 1989, 1990; van den Berk, Dirksen & Poot 2001; Stillman and others 2003). However, there is considerable experimental and field evidence that food deprivation can affect the tendency to move from a site. Empirical studies indicate that animals faced with unfavourable conditions which cause them to lose mass often exhibit pronounced changes in their behaviour once their reserves reach some lower critical threshold (Piersma & Poot 1992). Cold–weather movements of oystercatchers from eg The Wadden Sea (Hulscher 1989, 1990) are a prime example of a response to unfavourable environmental conditions. Thus, prior to reaching the point of starvation in The Wash under a given environmental scenario, an individual may choose to leave in search of more suitable feeding conditions. Thus, effectively the model predicts the proportion of the population that is not maintained in a positive energy balance by the shellfish resources and which might leave The Wash in search of alternative places to survive the winter. Model results need to be interpreted in this way rather as predictions of over-winter mortality *per se*.

6.1 Series 1 simulations

6.1.1 Percentage of bird populations supported

Eiders Under the present circumstances (Scenario 1) in which the stocks of cockles and mussels on the regulated beds are taken to be medium and *Ensis* stocks are high, the reduction of the total stock of the lay fishery to approximately 60 per cent of its current value is predicted to have no effect on the percentage of the eider population that is supported (Figure 6.1a). As the total lay stock is reduced below 50 per cent of the current value, however, the percentage of the eider population that is supported drops significantly and in the absence of any lay mussels, about 75 per cent of the 3,000 birds can be supported (Figure 6.1a). This pattern is virtually identical even if the stocks of shellfish on the cockle beds and regulated mussel beds are assumed to be low (Scenario 2) (Figure 6.1b) or indeed if the cockle stocks are set at historically low levels (Scenario 3) (Figure 6.1c). In contrast, under circumstances in which the stock of *Ensis* is taken to be low (and the shellfish stocks on the cockle beds and regulated mussel beds are taken to be medium) (Scenario 4), the percentage of the eider population that can be supported is reduced, even assuming no reduction to the abundance of lay mussels (Figure 6.1d). Under these circumstances, the reduction of the total stock of the lay fishery to 60 per cent of its current value is predicted to result in a further decline in the percentage of the eider population that is supported (Figure 6.1d). As the total lay stock is reduced further, the percentage of the eider population that is supported with only a low stock of *Ensis* drops very significantly and in the absence of any lay mussels, only about 10 per cent of the 3,000 birds can be supported (Figure 6.1d). This pattern is virtually identical even if the stocks of shellfish on the cockle beds and regulated mussel beds are assumed to be high (Scenario 5) (Figure 6.1e).

Oystercatchers In contrast to eiders, the percentage of the oystercatcher population that can be supported is independent of the total stock of lay mussels available to them, regardless of the abundance of the other shellfish resources (Figure 6.2). Moreover, variation in the abundance of the other shellfish resources appears to make very little difference to the percentage of the oystercatcher population that can be supported (Figure 6.2). The only exception to these generalisations occurs under Scenario 3 when the stock of regulated mussels was assumed to be low and the stock of cockles was ascribed historically low values equivalent to those seen in the poorest years of the early to mid 1990s (Figure 6.2c). Under these circumstances the percentage of the oystercatcher population that could be supported was reduced (max c 90 per cent) and declined further as the stock of lay mussels was reduced to very low levels. In the absence of lays, only 70-75 per cent of the population could be supported against this background of low natural shellfish resources. This is consistent with the predictions generated by the model of Stillman and others (2003) which predicted oystercatcher 'mortality' of between 20 per cent and 30 per cent when simulating the poorest years of the early-mid 1990s.

6.1.2 Distribution of predation pressure between resource types

The figures for the mean tonnage of live shellfish mass (including shells) removed over winter by eiders and oystercatchers from each of the four principal shellfish resources (ie lay mussels, regulated bed mussels, cockles and *Ensis*), as the scale of the lay fishery is reduced against each of five alternative shellfish resource backgrounds are illustrated in Figures 6.3 to 6.7 and presented in tabular format in Tables 6.1 and 6.2.

Eiders Under all five alternative scenarios, the total tonnage of lay mussels consumed by eiders declined as expected as the total tonnage available to them declined. This pattern was the same regardless of the background shellfish resources assumed in each of the five scenarios (Figure 6.3 – 6.7 (a)). In contrast, as the total tonnage of lay mussels available to the eiders declined the total tonnage of the other shellfish resources consumed increased, unless the stocks of these shellfish were assumed to be at a low level (Figure 6.3 – 6.7 (b,c & d)). The total consumption of lay mussels is predicted to reach its highest level if cockle and regulated mussel stocks remain as they are today but *Ensis* stocks were to crash to a low level again (Figure 6.6a). This probably reflects the fact that under this scenario the relative profitability of the lay mussels is maintained for longer than in the current situation with a healthy *Ensis* stock to switch to. Nonetheless, this increase in the loss of lay mussels occurs in spite of the reduced percentage of the eider population that can be supported under this scenario. The total consumption of lay mussels is also predicted to be greater than today if cockle and regulated mussel stocks return to the low values seen in the 1990s, even if *Ensis* were as abundant as today (Figure 6.4,6.5 (a)). In contrast, consumption of lay mussels is predicted to be somewhat less than today if the stocks of *Ensis* are low but the stocks of cockles and regulated mussels are high (Fig 6.7a). This reflects the increased profitability (and usage) of the cockle and regulated mussel stocks, but also the reduced percentage of the population of eiders that can be supported under this scenario. In other words, losses of lay mussels to eiders will be greater than today if one or other of the alternative shellfish resources is very scarce, and least whenever one of the alternative shellfish resource stocks is very abundant. As for the eiders' consumption of each of the alternative shellfish resources, this is generally highest when the stock of the resource in question is high while that of one of the others is low, and is generally lowest when the stock of the resource in question is low

while that of one of the others is high i.e. *Ensis* consumption increases when mussel and cockle stocks are low while mussel and cockle consumption increases when the *Ensis* stock is low (Figures 6.3-6.7 b,c,d). Thus, the extent to which eiders exploit each of the other non-lay mussel resources depends upon: i) the size of the lay mussel stock available to them and ii) the relative health of each of the alternative shellfish resources.

Oystercatchers Under all five alternative scenarios, the total tonnage of lay mussels consumed by oystercatchers declined as expected as the total tonnage available to them declined. This pattern was the same regardless of the background shellfish resources assumed in each of the five scenarios (Figure 6.3 – 6.7 (a)). In contrast to eider ducks, however, as the total tonnage of lay mussels available declined, the total tonnage of the other shellfish resources consumed by oystercatchers (which in every case far exceeded the consumption of lay mussels) scarcely changed at all (Figure 6.3 – 6.7 (b & c)).The consumption of lay mussels by oystercatchers is predicted to increase over present day values if the stocks of cockles and mussels on the regulated beds return to the low or very low values seen in the 1990s (Figure 6.4, 6.5 (a)). Consumption of lay mussels by oystercatchers is, however, not predicted to decrease if the stocks of cockles and mussels on the regulated beds reach high values again (Figure 6.7a). In other words, losses of lay mussels to oystercatchers will remain as today provided that the stocks of cockles and regulated mussels remain as healthy as or healthier than today but will increase if these stocks decline to historically low levels seen in the 1990s, but particularly if cockle stocks are very low. As for the oystercatchers' consumption of cockles or regulated mussels, their consumption of each one of these is generally highest when the stock of the resource in question is high relative to that of the other, whatever their absolute values (Figures 6.3-6.7 b,c). Thus, the extent to which oystercatchers exploit the cockle and regulated mussel stocks depends very little upon the size of the lay mussel stock available to them but upon the relative health of these two wild shellfish stocks.

Table 6.1 Predicted tonnage (live mass) of shellfish consumed by eider ducks over the course of the winter from each of four principal resource stocks as the total stock of lay mussels is reduced against five alternative background shellfish resource level scenarios (see Table 4.2 for details). Each value is a mean averaged across three replicate simulations.

	Percentage of current total stock of lay mussels remaining									
Resource	Scenario	0%	1%	5%	9%	20%	42%	60%	80%	100%
Lay mussels	1	0	0	108	172	308	362	503	564	643
	2	0	0	123	211	351	422	561	627	643
	3	0	0	124	211	348	440	556	629	635
	4	0	0	150	254	427	499	686	803	788
	5	0	0	139	199	353	362	458	523	560
Regulated mussels	1	88	88	70	66	65	64	54	44	0
	2	1	2	0	0	0	0	0	0	0
	3	1	2	0	0	0	0	0	0	0
	4	100	97	79	71	70	67	58	44	42
	5	323	307	246	227	187	186	161	161	164
Cockles	1	211	222	158	118	80	64	0	0	0
	2	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0
	4	366	380	308	330	280	275	116	24	6
	5	377	398	439	487	460	442	335	294	274
Ensis	1	362	364	321	314	247	237	162	133	133
	2	509	494	422	391	305	268	185	150	133
	3	524	487	417	392	313	282	180	141	132
	4	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0

Table 6.2 Predicted tonnage (live mass) of shellfish removed by oystercatchers over the course of the winter from each of four principal resource stocks as the total stock of lay mussels is reduced against five alternative background shellfish resource level scenarios (see Table 4.2 for details). Each value is a mean averaged across three replicate simulations.

	Percentage of current total stock of lay mussels remaining									
Resource	Scenario	0%	1%	5%	9%	20%	42%	60%	80%	100%
Lay mussels	1	0	15	35	66	81	89	93	116	134
	2	0	15	54	95	109	121	126	144	134
	3	0	16	69	145	185	208	242	257	274
	4	0	15	33	73	81	83	93	104	103
	5	0	15	33	70	79	82	95	112	99
Regulated mussels	1	1475	1466	1536	1516	1424	1486	1511	1391	1496
	2	1576	1519	1546	1579	1542	1543	1472	1544	1496
	3	2047	2043	2023	2009	1994	1975	1959	1969	1956
	4	1434	1498	1426	1528	1428	1409	1390	1500	1439
	5	1445	1530	1460	1476	1408	1368	1434	1413	1454
Cockles	1	2878	2850	2652	2631	2737	2593	2566	2826	2614
	2	2568	2715	2563	2380	2438	2336	2518	2377	2614
	3	1082	1083	1056	1044	1012	1052	1011	1032	1037
	4	2971	2799	2867	2610	2755	2807	2819	2577	2743
	5	2984	2773	2803	2725	2838	2871	2725	2718	2665
Ensis	1	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0

6.1.3 Distribution of predation pressure between lays

The figures for the mean tonnage of live mussel mass (including shells) removed from each of the lays over winter by eiders and oystercatchers as the scale of the lay fishery is reduced against each of five alternative shellfish resource backgrounds are illustrated in Figures 6.8 to 6.12 and presented in tabular format in Tables 6.3 and Table 6.4. To simplify the text in the following section no references are made to the precise figures which should be examined to see values relating to particular statements made. The reader should consult Tables 6.3 and 6.4.

Eiders Losses of mussels to eiders on the Roger lay are predicted to be greater than today if the stocks of cockles and regulated mussels were to fall to levels seen in the 1990s, even if *Ensis* stocks were to remain high. This is in spite of the fact that the percentage of the eider population that can be supported under these scenarios is not predicted to change (from baseline conditions). Losses of mussels to eiders on the Roger lay are predicted to be elevated to an even greater extent if *Ensis* were to crash to low levels again, even were cockle and

regulated mussel stocks to remain as today. This is in spite of the fact that the percentage of the eider population that can be supported is predicted to be lower than today under such circumstances. In contrast, losses of mussels to eiders on the Roger lay are predicted to be less than today if cockles and regulated mussels were to increase in abundance, even if *Ensis* stocks were to return to low levels. This is likely to be a reflection of the reduction in the percentage of the eider population that can be supported under this scenario. Thus, the losses of mussels from the Roger lay due to eider predation are predicted to vary depending upon the abundance of all other shellfish resources.

Losses of mussels to eider ducks on the Toft lay are predicted to be the same as today, regardless of whether the stock of regulated mussels and cockles declines, provided that the stock of *Ensis* remains high. This reflects the lack of any change in the percentage of the eider population that can supported under these alternative scenarios. However, if the stock of *Ensis* were to decline to a low level, the losses from the Toft lay are predicted to increase irrespective of whether the stocks of regulated mussels or cockles improve over current day stocks. This is in spite of the fact that the percentage of the eider population that can be supported is predicted to be lower than today under such circumstances. Thus, the losses of mussels from the Toft lay due to eider predation are predicted to vary depending primarily upon the abundance of the *Ensis* resource.

Losses of mussels to eider ducks on the Clay Hole and Scotsman's Sled lays are predicted to remain virtually the same under all circumstances except that in which the stock of *Ensis* is assumed to decline in the absence of any increase in the stock of cockles and regulated mussels. Under this scenario losses from the Clay Hole and Scotsman's Sled lays are predicted to increase. Eiders are not predicted to utilise either the Black Buoy or Herring Hill lays to any significant extent under any scenario even when these are the only two lays remaining in the system.

The only circumstance in which losses of mussels to eiders from a particular lay is predicted to be lower than under current circumstances is the decline in the predicted losses from the Roger lay if cockles and regulated mussels were to become more abundant than today in combination with a decline in *Ensis* stocks. This decline in predation is probably a consequence of the increased exploitation by eiders of the relatively more profitable cockle and regulated mussels under this scenario but also ultimately the reduction in the percentage of the eider population that can be supported in the absence of a healthy *Ensis* stock.

The pattern of change in the loss to eider ducks from a given lay as the total stock of lay mussels is gradually reduced is affected very little by the background resource levels available on the other shellfish beds. As the stock on the Roger lay is reduced, the tonnage taken from there by eiders also reduces whereas the predation pressure on the Toft lay (and indeed the other lays) remains unchanged until the Roger lay is removed completely. Once the Roger lay is removed completely, the predation pressure on the Toft, Clay Hole and Scotsman's sled lays is predicted to increase dramatically. As the stock on the Toft lay is then reduced, losses to eiders from the Toft lay diminish too while the predation pressure exerted by eiders on the Clay Hole and Scotsman's sled lays increases further. Losses on the Scotsman's sled lay are predicted to increase further as the stock on the Clay Hole lay is removed. Thus, with the exception of the Black Buoy and Herring Hill lays, where the very low numerical density of

mussels probably renders them unsuitable as eider foraging habitat, the gradual shrinkage in the extent of the commercially cultivated mussel lays in The Wash, starting with the most heavily used, is predicted to result in a spreading out of eider predation pressure on to the remaining lays.

Oystercatchers Losses of mussels to oystercatchers from lays are considerably less than losses to eider ducks under all circumstances. Losses from all lays are predicted to be very similar to those under the current circumstances provided that the stocks of cockles and regulated mussels remain as healthy as today or increase in abundance, even if *Ensis* stocks (on which oystercatchers are assumed not to feed) crash. In contrast, losses from all lays (with the exception of Black Buoy and Herring Hill) are predicted to increase if the stocks of cockles and regulated mussels were to decline to the low values seen in the early-mid 1990s. This is especially so if the cockles are predicted to fall to very low levels, in spite of the predicted decrease in the percentage of the oystercatcher population that can be supported throughout the winter under this scenario. Losses to oystercatchers from Black Buoy are predicted to be constant under all circumstances and they are not predicted to utilise Herring Hill under any circumstance. Thus, the predation pressure exerted by oystercatchers on the principal commercially cultivated mussel lays today is unlikely to change significantly if cockles and regulated mussel stocks remain as they are today or indeed increase in abundance but are predicted to increase if the stocks of these shellfish were to decline significantly.

The pattern of change in the loss to oystercatchers from the Roger and Toft lays as the total stock of lay mussels is gradually reduced, is unaffected by the background shellfish resource levels. The increase in the loss to oystercatchers from the Clay Hole and Scotsman's sled lays as the total stock of lay mussels is gradually reduced, is more pronounced only if the stock of cockles is set at historically low levels. In the case of all other lays under all other circumstances, the gradual loss of lays makes no difference at all to the predation pressure exerted on them by oystercatchers. Thus, the gradual shrinkage in the stock on the commercially cultivated mussel lays in The Wash, starting with those most heavily used (by eiders), is predicted to make very little difference to the predation pressure exerted by oystercatchers on the remaining lays unless cockles are very scarce. It is only under these circumstances that the lays are utilised to any great extent by oystercatchers.

Table 6.3 Predicted tonnage (live mass) of mussels consumed by eider ducks over the course of the winter from each of four lays as the total stock of lay mussels is reduced against five alternative background shellfish resource level scenarios (see Table 4.2 for details). Each value is a mean averaged across three replicate simulations.

Lay	Scenario	Percentage of current total stock of lay mussels remaining								
		0%	1%	5%	9%	20%	42%	60%	80%	100%
Roger	1	0	0	0	0	0	0	405	475	514
	2	0	0	0	0	0	0	452	534	552
	3	0	0	0	0	0	0	451	536	546
	4	0	0	0	0	0	0	503	684	673
	5	0	0	0	0	0	0	346	409	442
Toft	1	0	0	0	0	160	223	91	88	91
	2	0	0	0	0	188	273	94	91	90
	3	0	0	0	0	190	292	93	92	89
	4	0	0	0	0	235	334	118	118	114
	5	0	0	0	0	194	231	111	114	118
Clay Hole	1	0	0	0	92	79	75	4	0	0
	2	0	0	0	111	90	80	9	0	0
	3	0	0	0	109	83	77	6	0	0
	4	0	0	0	135	102	88	36	0	0
	5	0	0	0	105	85	71	1	0	0
Scotsman's Sled	1	0	0	108	79	68	63	2	1	1
	2	0	0	123	101	76	69	7	1	1
	3	0	0	124	102	75	71	6	1	1
	4	0	0	150	119	90	76	29	1	1
	5	0	0	139	95	74	60	1	1	1

Table 6.4 Mean predicted tonnage (live mass) of mussels removed by oystercatchers over the course of the winter from each of five lays as the total stock of lay mussels is reduced against five alternative background shellfish resource level scenarios (see Table 4.2 for details). Each value is a mean averaged across three replicate simulations

Lay	Scenario	Percentage of current total stock of lay mussels remaining								
		0%	1%	5%	9%	20%	42%	60%	80%	100%
Roger	1	0	0	0	0	0	0	19	36	35
	2	0	0	0	0	0	0	23	39	41
	3	0	0	0	0	0	0	47	71	92
	4	0	0	0	0	0	0	20	32	36
	5	0	0	0	0	0	0	19	35	31
Toft	1	0	0	0	0	15	22	9	14	6
	2	0	0	0	0	17	28	18	19	9
	3	0	0	0	0	53	82	76	69	65
	4	0	0	0	0	14	18	11	10	8
	5	0	0	0	0	14	17	14	13	7
Clay Hole	1	0	0	0	33	34	35	32	35	33
	2	0	0	0	45	45	41	42	40	42
	3	0	0	0	78	72	68	65	63	63
	4	0	0	0	36	35	34	33	32	32
	5	0	0	0	36	34	34	33	33	32
Scotsman's Sled	1	0	0	20	18	16	17	18	17	16
	2	0	0	38	35	31	36	27	31	27
	3	0	0	53	50	44	43	38	39	37
	4	0	0	18	21	17	17	15	16	14
	5	0	0	17	18	15	16	15	16	15
Black Buoy	1	0	15	15	15	16	15	15	15	14
	2	0	15	16	15	16	15	16	16	15
	3	0	16	16	17	16	15	16	16	16
	4	0	15	15	16	15	15	15	15	14
	5	0	15	16	15	15	15	15	15	14

6.2 Series 2 simulations

In these simulations we explore the effect of changes to the way in which the existing stock of lay mussels (c 10,000t) is distributed on the percentage of the two populations of birds that can be supported and on the magnitude of the predation pressure exerted by those birds on the various shellfish resources. These simulations are conducted against two alternative backgrounds in both of which the stock of shellfish on the cockle beds and regulated mussel beds are assumed to be as they are today but in which the stock of *Ensis* is either abundant (10,000t) or scarce (1,000t).

6.2.1 Percentage of bird populations supported

Eiders In the presence of an abundant stock of *Ensis*, concentrating the lay mussel stock into a smaller area by halving the area of each of the lays but doubling the numerical density of the mussels within those areas (to hold the total stock the same) (Scenario 2a) had no effect on the percentage of the eider population that could be supported. This remained in excess of 95 per cent (Figure 6.13a). In contrast, spreading the lay mussel stock over a larger area by doubling the area of each of the lays while halving the numerical density of the mussels within those areas (to hold the total stock the same) (Scenario 2b) resulted in a significant reduction in the percentage of the eider population that could be supported (Figure 6.13a). Removing any 'hotspots' by equalising the numerical density of mussels across all the lays (Scenarios 2c and 2d) also resulted in a significant reduction in the percentage of the eider population that could be supported in comparison to the baseline scenario (Fig 6.13a).

In the absence of a healthy stock of *Ensis*, the effect of changes to the way in which the existing stock of lay mussels is distributed had more pronounced effects on the eider population (Figure 6.13c). Concentrating the lay mussel stock into a smaller area by halving the area of each of the lays but doubling the numerical density of the mussels within those areas (Scenario 2a) significantly increased the percentage of the eider population that could be supported over the somewhat reduced value predicted if the lays were organised as they are today (Figure 6.13c). Spreading the lay mussel stock over a larger area by doubling the area of each of the lays while halving the numerical density of the mussels within those areas (Scenario 2b) resulted in a very pronounced reduction in the percentage of the eider population that could be supported (Figure 6.13c). In the absence of an abundant *Ensis* stock, removing any lay 'hotspots' by equalising the numerical density of mussels across all the lays (Scenarios 2c and 2d) also resulted in significant, reductions in the percentage of the eider population that could be supported (Figure 6.13c).

Oystercatchers In contrast to eiders, the percentage of the oystercatcher population that can be supported is predicted to be independent of any changes to the way in which the existing stock of lay mussels is distributed within and between the six principal lays (Figure 6.13b,d). This reflects the very minor use of these resources by the oystercatchers.

6.2.2 Distribution of predation pressure between resource types

The figures for the mean tonnage of live shellfish mass (including shells) removed from each of the principal shellfish resource stocks over winter by eiders and oystercatchers under each of five alternative lay management scenarios and two alternative background shellfish resource levels are illustrated in Figure 6.14 and presented in tabular format in Tables 6.5 and 6.6.

Eiders When set against the current background of medium cockle stocks and regulated mussels stocks and a high stock of *Ensis*, doubling the numerical density of mussels on all

lays simultaneously while halving their areas (Scenario 2a) resulted in losses of lay mussels to eider ducks increasing from c 606 tonnes to c 660 tonnes (Figure 6.14a). This was a result primarily of increased predation pressure on Roger (see section 6.2.3) and was accompanied by a slightly reduced usage of regulated mussel beds and *Ensis* stocks (Figure 6.14a). In contrast, halving the numerical density of mussels on all lays simultaneously while doubling their areas (Scenario 2b), resulted in losses of lay mussels to eider ducks decreasing to their lowest values (c 400 tonnes) (Figure 6.14a). This was accompanied by an increased usage of the other resources, especially *Ensis*. This decline in the overall predation pressure exerted by eider ducks on the lays reflected the decline in the percentage of the population that could be supported ie spreading lay mussels out will reduce losses to eiders but put an increasing proportion of the eider population 'at risk'. Equalising the numerical density of mussels across all lays (Scenario 2c) or making the lays identical in all respects (Scenario 2d) also reduced the overall losses of lay mussels to eider ducks (to c 500 tonnes) and increased usage of the other shellfish resources. These intermediate values of overall losses from the lays as a whole reflected change to the distribution of predation pressure between the lays (see 6.2.3). Even so, the removal of 'hot spots' resulted in a decline in the percentage of the population of eider that could be supported. Thus, in summary, increasing the extent to which the lay mussel resources are aggregated increases their profitability to eider ducks and results in increased losses from them. Reducing the numerical density of mussels by spreading mussels more thinly on all lays will decrease the predation pressure on the lays and increase the birds' reliance on other resources, but result in a decrease in the percentage of the eider population that can be supported.

When the same set of scenarios were conducted against a background in which the stock of *Ensis* was assumed to have crashed to a low level, the total loss of mussels due to eider predation across all lays was greater under each scenario than when the *Ensis* stock was assumed to be high (Figure 6.14 a,b). This was in spite of the fact that, with the exception of scenario 2a, the percentage of the eider population that could be supported was predicted to be lower than when the *Ensis* stock was assumed to be healthy (Figure 6.13 a,c). These elevated losses probably reflect the lack of a healthy stock of *Ensis* to which the eider duck could switch. However, one important difference to the results described above, is that in the absence of a healthy *Ensis* stock to which eider ducks could switch, doubling the lay stock densities and halving the lay areas did not result in any further increase in the losses of lay mussels (c 790 tonnes in both cases) (Figure 6.14b). Indeed, in the absence of a healthy *Ensis* stock, losses from the lays were remarkably similar under each scenario, except that in which the stock densities were halved and lay areas doubled (Scenario 2b) when (as in the presence of a healthy *Ensis* stock) the losses from the lays reached their lowest values (Figure 6.14b) as did the percentage of the eider population that could be supported (Figure 6.13c). Thus, in summary, if the stock of *Ensis* were to crash to a low level again, the total loss of lay mussels to eiders is predicted to increase. However, under these circumstances increasing the extent to which the lay mussel resources are aggregated will not further increase losses to eiders. Nonetheless, under these circumstances reducing the numerical density of mussels by spreading mussels more thinly on all lays could return the losses of lay mussels to present day values but will probably result in a marked decrease in the percentage of the eider population that can be supported.

Oystercatchers As would be expected, doubling the numerical density of lay mussels while halving the lay areas (scenario 2a) produced a minor decrease in the losses of lay mussels to

oystercatchers while the opposite was true if the densities of mussels were halved and bed areas doubled (scenario 2b) (Figure 6.14c,d). However, the magnitude of this change was very small. In contrast to eiders, the tonnage of shellfish removed by oystercatchers from each of the other principal shellfish resources available to them was very little changed by alteration to the way in which the existing stock of lay mussels is distributed within and between the six principal lays (Figure 6.14 c). This was true irrespective of the state of the *Ensis* stock (Figure 6.14 c,d). There were much more pronounced effects on the distribution of oystercatcher predation between lays (section 6.2.3).

Table 6.5 Predicted tonnage (live mass) of shellfish consumed by eider ducks over the course of the winter from each shellfish resource under five alternative lay management scenarios and against two alternative backgrounds in which the stock of *Ensis* is assumed to be high (as today) or low (see section 4.2.2. for details). Each value is a mean averaged across three replicate simulations.

Ensis stock level	Scenario	Shellfish resource			
		Lay mussels	Regulated mussels	Cockles	*Ensis*
High (10,000t)	Baseline	606	41	0	128
	2a	660	19	0	85
	2b	398	61	28	239
	2c	532	61	5	144
	2d	480	57	4	188
Low (1,000t)	Baseline	788	42	6	0
	2a	788	19	0	0
	2b	655	63	183	0
	2c	785	61	27	0
	2d	713	64	66	0

Table 6.6 Predicted tonnage (live mass) of shellfish removed by oystercatchers over the course of the winter from each shellfish resource under five alternative lay management scenarios and against two alternative backgrounds in which the stock of *Ensis* is assumed to be high (as today) or low (see section 4.2.2. for details). Each value is a mean averaged across three replicate simulations.

Ensis stock level	Scenario	Shellfish resource			
		Lay mussels	Regulated mussels	Cockles	*Ensis*
High (10,000t)	Baseline	105	1408	2742	0
	2a	89	1463	2689	0
	2b	131	1371	2689	0
	2c	108	1414	2672	0
	2d	119	1404	2729	0
Low (1,000t)	Baseline	103	1439	2743	0
	2a	90	1506	2632	0
	2b	132	1406	2667	0
	2c	109	1431	2773	0
	2d	134	1392	2706	0

6.2.3 Distribution of predation pressure between lays

The figures for the mean tonnage of live mussel mass (including shells) removed from each of the lays over winter by eiders and oystercatchers under each of five alternative lay management scenarios and two alternative background shellfish resource levels are illustrated in Figure 6.15 and presented in tabular format in Tables 6.7 and 6.8.

Eiders When set against the current background of medium cockle stocks and regulated mussels stocks and a high stock of *Ensis*, doubling the numerical density of mussels on all lays simultaneously while halving their areas (Scenario 2a) resulted in losses of mussels to eider ducks increasing on the Roger lay (559 tonnes compared to 514 tonnes). Losses on Toft changed very little while the other lays were, as under current conditions, not predicted to be exploited at all by eider ducks (Figure 6.15a). Thus, concentrating the mussel resources increased the exploitation of the best patch. In contrast, halving the numerical density of mussels on all lays simultaneously while doubling their areas (Scenario 2b) resulted in losses of mussels to eider ducks decreasing on both Roger (378 tonnes) and Toft lays but no spreading of predation pressure to the other lays which were still relatively unattractive in comparison with Roger and Toft (Figure 6.15a). This decline in the overall predation pressure exerted by eider ducks on the lays under this scenario reflected the decline in the percentage of the population that could be supported ie spreading lay mussels out will reduce losses to eiders but put an increasing proportion of the eider population 'at risk'. Equalising the numerical density of mussels across all lays (Scenario 2c) resulted in a further drop in the losses to eiders on the Roger Lay (201 tonnes), but a marked increase everywhere else such that all lays were now predicted to be exploited to some degree (Figure 6.15a). This change reflects the fact that under current conditions the numerical density of mussels and hence the attractiveness of the Roger lay to eiders far exceeds that of any of the others. The removal of this 'hot spot' resulted in a marked decline in the percentage of the eider population that could be supported. When the six principal lays were made identical (in terms of numerical density of mussels, area and shore height) the losses to eiders were, as expected, equalised too (c 80 tonnes from each lay) (Figure 6.15a). Due to the lack of any really profitable lay area under this scenario, the total loss from the lays was lower than under the present arrangements and the percentage of the eider population that could be supported was reduced. Thus, in summary, increasing the extent to which the lay mussel resources are aggregated increases the profitability of the best lay areas to eider ducks and results in increased losses from them. Reducing the numerical density of mussels by spreading mussels more thinly on all lays will decrease the predation pressure on the best lays but not result in any spread of predation to the still relatively poorer lays. Making the lays more similar to one another by evening out variations in numerical density of mussels, areas and shore height will even out eider predation pressure too but probably at the expense of decreasing the percentage of the eider population that can be supported.

When the same set of scenarios were conducted against a background in which the stock of *Ensis* was assumed to have crashed to a low level, the total loss of mussels due to eider predation across all lays was greater than when the *Ensis* stock was assumed to be high (Figure 6.15a,b). However, changes to the way in which the mussel resources were distributed resulted in more or less the same changes to the distribution of predation pressure between lays as when the stock of *Ensis* was assumed to be high (Figure 6.15 a,b). Thus, the summary

of the results described above apply regardless of the health of the *Ensis* stock. It should be borne in mind, however, that changes to the way in which the lay mussels were distributed had a much more pronounced effect on the percentage of the eider population that could be supported under circumstances in which the *Ensis* stock was assumed to be low (Figure 6.13a,c).

Oystercatchers When set against the current background of medium cockle stocks and regulated mussels stocks and a high stock of *Ensis*, doubling the numerical density of mussels on all lays simultaneously while halving their areas (Scenario 2a) resulted in losses to oystercatchers decreasing on the Roger and Clay Hole lays but little change on the other lays (Figure 6.15c). This reflects the fact that the improvement in the interference free intake rate (IFIR) available on these two lays with the highest numerical density of mussels will have been improved only a little by increasing the density of mussels even further whereas, as on all beds, the halving of the areas will have increased the intensity of interference competition amongst oystercatchers. On Roger and Clay Hole this will have overridden any slight improvement in the IFIR available. In contrast, halving the numerical density of mussels on all lays simultaneously while doubling the lay areas (Scenario 2b), resulted in losses of mussels to oystercatchers increasing on the three lays with the highest mussel density ie Roger, Clay Hole and Scotsman's sled, while losses from the other three lays remained unchanged (Figure 6.15c). This probably reflects the relatively slight reduction in the IFIR available on these three best beds combining with a reduced strength of interference to make them relatively more attractive. Equalising the numerical density of mussels across all lays (Scenario 2c) resulted in a slight reduction in the losses to oystercatchers on Roger (relative to baseline), a slight increase on Black Buoy and no change elsewhere (Figure 6.15c). These changes arise from Roger having the highest numerical density and Black Buoy the lowest under current conditions and hence these being the beds most affected by equalisation of mussel density. When the six principal lays were made identical (in terms of numerical density of mussels, area and shore height) (scenario 2d) the losses to oystercatchers were not exactly equalised due to the assumed faithfulness of birds to particular regions of The Wash. However, losses on Roger were reduced to their lowest level as were those on Black Buoy. These changes reflect the reduction in the size of the Roger lay and the effective down shore movement of the Black Buoy lay. In contrast, losses on Clay Hole and Scotsman's sled reached their highest levels under this scenario (Figure 6.15c). This reflects the assumed increase in the size of these lays under this scenario.

Thus, in summary, increasing the extent to which the lay mussel resources are aggregated reduces the profitability of the best areas to oystercatchers, due to increasing the levels of interference competition, and results in decreased losses from the best areas. Reducing the numerical density of mussels by spreading mussels more thinly on all lays will increase the predation pressure on the best lays but not result in any spread of predation to the still relatively poorer lays. The effect of changes to the way in which mussels are distributed on the predation pressure exerted by oystercatchers is therefore the opposite of that on the predation pressure exerted by eiders ducks. This reflects the existence of interference competition in oystercatchers and its assumed absence in the case of eider ducks. Making the lays more similar to one another by evening out variations in numerical density of mussels, areas and shore height will even out oystercatcher predation pressure to an extent. The most noticeable effects will be seen on beds that are currently extreme in terms of their area, mussel density or shore height. It should be noted that all of these manipulations had no effect

on the percentage of the oystercatcher population that can be supported (Figure 6.13b) and that the overall losses of lay mussels to oystercatchers under all scenarios are far lower than those to eider ducks. Given that oystercatchers are assumed not to consume *Ensis*, the results of conducting these alternative lay management scenarios against a background in which *Ensis* stocks were assumed to be low, were exactly the same as described above (Figure 6.15d).

Table 6.7 Predicted tonnage (live mass) of mussels consumed by eider ducks over the course of the winter from each lay under five alternative lay management scenarios and against two alternative backgrounds in which the stock of *Ensis* is assumed to be high (as today) or low (see section 4.2.2. for details). Each value is a mean averaged across three replicate simulations.

Ensis stock level	Scenario	Mussel lay					
		Roger	Toft	Clay Hole	Scotsman's sled	Black Buoy	Herring Hill
High (10,000t)	Baseline	514	91	0	1	0	0
	2a	589	100	0	1	0	0
	2b	378	20	0	1	0	0
	2c	201	176	47	37	24	45
	2d	81	83	75	78	83	80
Low (1,000t)	Baseline	673	114	0	1	0	0
	2a	680	107	0	1	0	0
	2b	538	117	0	1	0	0
	2c	271	255	53	44	25	135
	2d	121	122	112	118	121	118

Table 6.8 Predicted tonnage (live mass) of mussels removed by oystercatchers over the course of the winter from each lay under five alternative lay management scenarios and against two alternative backgrounds in which the stock of *Ensis* is assumed to be high (as today) or low (see section 4.2.2. for details). Each value is a mean averaged across three replicate simulations

Ensis stock level	Scenario	Mussel lay					
		Roger	Toft	Clay Hole	Scotsman's sled	Black Buoy	Herring Hill
High (10,000t)	Baseline	35	6	33	16	14	0
	2a	26	10	24	13	15	0
	2b	40	6	49	22	14	0
	2c	30	7	35	16	20	0
	2d	5	5	56	23	5	25
Low (1,000t)	Baseline	36	8	32	14	14	0
	2a	27	11	24	12	16	0
	2b	39	7	50	24	13	0
	2c	32	7	34	16	21	0
	2d	11	11	55	23	11	25

6.3 Series 3 simulations

In the absence of commercially cultivated mussel lays and in the absence of significant stocks of *Ensis directus*, the percentage of the eider population that is not supported is predicted to exceed a typical overwinter mortality value of 5 per cent and indeed an exceptionally high value of 15 per cent, regardless of the size of the peak eider population (Figure 6.16a). Thus, in the absence of these two shellfish resources that are not part of the 'natural' Wash ecosystem, the size of the eider population that can be supported with an acceptable level of 'mortality' is very much reduced. In the absence of these two highly profitable resources, the availability of abundant cockle and wild mussel stocks is, primarily due to their comparatively poor energetic profitability, not sufficient to support the bulk of any size of eider population. Even with the addition of an abundant stock of *Ensis directus*, the absence of commercially cultivated mussel lays is still predicted to seriously limit the size of the peak population of eiders that can be supported without more than 5 per cent of the population being at risk (Figure 6.16b). In the presence of the lays as they are today, but in the absence of an abundant *Ensis directus* stock, a peak population of around 2,000 eiders is predicted to be supported without any more than a 'typical' 5 per cent being at risk of mortality (Figure 6.16c). Thus, it would seem to be the presence of a thriving commercial mussel growing industry that affords the possibility of a large population of eiders being supported without an excessive proportion being at risk of mortality. When a large stock of commercially cultivated lay mussels is combined with a healthy stock of *Ensis directus* (against a background of abundant cockle (50,000t) and wild mussel (20,000t) stocks), a peak population of 10,000 - 12,000 eider ducks is predicted to be supported without the percentage at risk of mortality exceeding 5 per cent (Figure 6.16d).

7. Discussion

7.1 Validation simulations

The first of the key areas of future work identified by Defra in advance of the public inquiry in summer 2006 (see section 1.1) was addressed by a program of aerial surveys of The Wash conducted between November 2005 and March 2006 by the Wildfowl and Wetlands Trust (Smith, Hall, Worden, Harrison, Allen, Bradbury, Cranswick, Woodward, Shepherd, Paynter & McGill 2006). The third and fourth areas were addressed by a small-scale trial involving the use of three electronic wailers, combined with other scaring technologies, on three lays on Roger/Toft, where most mussel predation by eider ducks was reported. This work was conducted by the Bird Management Unit of the Central Science Laboratories (Hart & Brown 2006). In combination, these two studies confirmed the marked concentration of eider ducks on the commercially cultivated mussel lays in the Roger/Toft area which has been noted by the fishermen in recent years.

One of the principal ways in which the model MORPH (and its predecessors) has been validated has been to determine whether the model can generate a distribution of birds that matches that observed in the real world. This is always a valid test of these models because within each model each birds' usage of the patches available to them is NOT forced upon them but is the RESULT of each individual within the model population following simple behavioural rules to DECIDE where the best place to feed is at each point in time. In the present study, the model MORPH was parameterised primarily with shellfish data collected from The Wash in 2005-2006 in order to mimic the current distribution, abundance and quality of shellfish resources available to eiders and oystercatchers in The Wash. The distribution of eiders that it generated was exactly in accord with that which has been observed ie nearly 75 per cent of the eiders in reality and in the model were predicted to occur in Region 2 ie that including the Roger and Toft lays. Eiders were rarely seen in other regions of The Wash and were not predicted by the model to occur there to any great extent. This validation test (in combination with the others described in section 5) provides considerable confidence that the model accurately mimics the most important aspects of The Wash system. Accordingly, we can have some confidence in discussing the predicted implications of changes to the scale of the lay cultivation industry and the way in which it is managed, against a number of alternative background shellfish resource scenarios, as described in the following sections.

7.2 Series 1 simulations

This series of simulations was conducted in order to establish the implications for the current overwintering populations of eider ducks and oystercatchers of a decline in the abundance/availability of lay mussel resources from the current high level. Such declines could arise either as a result of scaring devices being deployed across the lays or following a market-led reduction in the scale of the commercially cultivated mussel-growing industry. Simulations were conducted not just against the present day background of the alternative shellfish resources to which birds could switch, but against a number of other alternatives in which the abundance of these shellfish stocks were varied in line with past records. This was

necessary to establish whether the implications of changes to the abundance/availability of lay mussel resources might vary under circumstances that might reasonably be expected to arise in the future of The Wash.

7.2.1 Eiders

Percentage of population supported The principal finding of these simulations is that, regardless of the background abundance of alternative, native, wild shellfish resources, the percentage of the current population of eiders that can be supported is dependent upon the abundance of the mussels available to them on the commercially cultivated lays. Against all backgrounds, the percentage of the eider population that could be supported declined as the total stock of lay mussels available to them declined. However, the relationship was not linear in any case and the magnitude of the decline varied between scenarios in which the background shellfish resources varied. Provided that the stock of *Ensis* was assumed to be healthy, the lay stock available to eiders could be reduced by up to 50 per cent without any significant effect upon them. However, if the lay stock was reduced below this point, even with a healthy stock of *Ensis*, the percentage of the eider population that could be supported was predicted to decline significantly. If the stock of *Ensis* were to decline to low levels again in the future, which is quite likely given their intermittent pattern of recruitment and short life span (Palmer 2003), the eider population will be far more vulnerable to any loss of lay mussel resources. In contrast, future variation in the abundance of cockles or mussels on the regulated beds appears to be unlikely to significantly alter the effect on eider ducks of changes to the abundance of lay mussels. Thus, the continued well being of the current high population of eiders is dependent upon the continued health of the *Ensis* stock and continued access to a considerable fraction of the existing lay mussel stock.

Distribution of predation pressure between alternative shellfish resources Under current circumstances the model predicted that eiders consume approximately 600 – 650 tonnes of mussels from the commercially cultivated lays, principally from Roger and Toft. This is considerably lower than the losses of 90 per cent of 1,600 tonnes of mussels attributed to eiders (English Nature 2005). It is also considerably lower than the worst case scenario of 214 tonnes per month (ie 856 tonnes over a four month period or 1,494 tonnes over a seven month period) calculated in the appropriate assessment (English Nature 2005). Nonetheless, 600 - 650 tonnes constitutes a significant proportion of the mussels apparently lost from the lays. It should be borne in mind that this figure only relates to the tonnage of mussels actually consumed by eiders to meet their energetic requirements. It does not account for any mussels that might be lost as result of eider foraging activity but not consumed by them. Eiders feeding on mussels in the wild must break the mussel's byssal attachment to the substrate and neighbouring mussels and then often select a single mussel to be swallowed from a clump that has been detached together. The other mussels, having lost their attachment to the bed, may then be vulnerable to being washed off the lays. In this way the total tonnage of mussels lost due to eider activity could exceed the amount that they actually consume. However, mussels, including adults, can rapidly secrete new byssal threads to reattach themselves to the substrate. It is not possible at present to be sure of the relationship between mussel consumption by eider ducks and the total tonnage that is lost from commercially cultivated lays as a result of their foraging activity.

The model predicts that as the abundance of lay mussels available to eiders is reduced the losses of lay mussels to eiders will decline regardless of the abundance of the other shellfish resources. However, at any given level of lay stock, losses of lay mussels to eider ducks will be greater than today if any of the alternative shellfish resources, especially *Ensis*, were to crash to low levels seen in the past. Under all of the alternative background shellfish resource scenarios, a decline in the abundance of their preferred resource ie lay mussels was predicted to lead to increasing usage of the alternative resources by eider ducks. The extent to which eiders exploited these alternative resources depended upon their relative abundance. When a high stock of *Ensis* was available, this was the resource to which eiders switched primarily as the stock of lay mussels was reduced. However, if *Ensis* was scarce, eiders were predicted to switch to cockles and regulated mussel stocks particularly if these were abundant. Thus, under present circumstances, the bulk of the food consumed by eiders comes from the commercially cultivated mussel lays. If the abundance of this resource available to eiders is reduced, due either to birds being excluded from the lays, or a reduction in the scale of the fishery, eider will switch to alternatives. This will not be sufficient to ensure that the percentage of the population that can be supported will be maintained even with a healthy stock of *Ensis* or a healthy stock of cockles and regulated mussels.

Distribution of predation pressure between commercially cultivated lays The model predicts that under current circumstances, the bulk of the tonnage of lay mussels consumed by eiders is taken from the Roger Lay (514 tonnes) and the remainder (91 tonnes) from the Toft lay. This is entirely in accord with the real-world situation. The model predicts that losses from the Roger and Toft lays will increase if the stocks of cockles and regulated mussels were to decline to historically low levels seen in the 1990s or *Ensis* stocks were to crash in the absence of very abundant cockles and regulated mussel stocks. Thus, although the losses from these two lays may be considered unacceptable, they are probably lower than they might otherwise be due to the availability of at least one other very healthy shellfish stock in The Wash.

The gradual decline in the abundance of the lay mussel stock available to eiders brought about by the sequential loss of access to beds starting with those that are currently most heavily used (ie Roger and Toft), resulted in a spreading out of eider predation pressure on to the remaining lays, principally Scotsman's Sled and Clay Hole. This spreading of the predation pressure across the lays, and indeed to other shellfish stocks, was not sufficient to ensure that the percentage of the population that can be supported will be maintained even with a healthy stock of *Ensis* or a healthy stock of cockles and regulated mussels.

7.2.2 Oystercatchers

Percentage of population supported The results of the 2002-2003 low tide survey of The Wash (Yates, Garbutt, Rispin & Brown 2004) indicated that the Roger/Toft area of The Wash is an important feeding area for many wading species of birds including oystercatchers (English Nature 2005). Six percent of the population of oystercatchers occurred in this area and distribution maps produced by Yates, Garbutt, Rispin & Brown (2004) indicated that this species is concentrated on the Toft lay areas or their close vicinity. The lay areas represent the main feeding area for oystercatchers on Roger/Toft. In spite of this fact, the model predicts

that, in contrast to eiders, the percentage of the oystercatcher population that can be supported does not decline at all as the total stock of the lay fishery mussels available to them declines against all but one background shellfish stock scenario. Only when the stock of regulated mussels was assumed to be low and the stock of cockles was ascribed historically low values (equivalent to those seen in the poorest years of the early to mid 1990s (ie c 4,000t)) was the percentage of the oystercatcher population that could be supported predicted to decline as the abundance of the lay stock was reduced. Against this background the percentage of the oystercatcher population that could not be supported in the complete absence of lays reached c 25 per cent. This is in very close agreement with the model results of Stillman and others (2003). Thus, given most likely future scenarios, the population of oystercatchers, unlike that of eiders, is not predicted to be vulnerable to changes to the abundance of the lay mussel resource. This reflects the relatively minor use of this habitat by oystercatchers (c 6 per cent) in comparison to eiders (c 75 per cent) and suggests that oystercatchers displaced from feeding on lays could be accommodated elsewhere in The Wash under most circumstances.

Distribution of predation pressure between alternative shellfish resources Under current circumstances the model predicted that oystercatchers remove approximately 100 - 150 tonnes of mussels from the commercially cultivated lays. Thus, in spite of the oystercatcher peak population being five fold greater than that of eiders they have a comparatively minor impact on the commercially cultivated mussel beds. The model predicts that if the abundance of lay mussels is reduced the losses of lay mussels to oystercatchers will decline regardless of the abundance of the other shellfish resources. However, at any particular value for the abundance of the lay stock, the consumption of lay mussels by oystercatchers is predicted to remain the same as under current circumstances provided that the stocks of cockles and regulated mussels remain as healthy as or healthier than today. Losses to oystercatchers will, however, increase if these stocks decline to the historically low levels seen in the 1990s. In contrast to eiders, the extent to which oystercatchers exploit the cockle and regulated mussel stocks depends very little upon the quantity of the lay mussel stock available to them but only upon the relative health of the two wild shellfish stocks.

Distribution of predation pressure between commercially cultivated lays The model predicts that under current circumstances, oystercatchers consume mussels from each of the principal lays. This reflects the fact that in the model, oystercatchers were attributed to regions around The Wash such that all of the principal lays were exploited rather than just the single most profitable one. At any particular value for the abundance of the total lay stock, the consumption of mussels by oystercatchers from any individual lay is predicted to remain the same as under current circumstances provided that the stocks of cockles and regulated mussels remain as healthy as or healthier than today but to increase if these stocks decline to the historically low levels seen in the 1990s. In contrast to eiders, the gradual decline in the abundance of the lay mussel stock brought about by the sequential loss of access to beds starting with the currently most heavily used (by eiders) did not result in a spreading out of oystercatcher predation pressure on to the remaining lays, unless cockles were very scarce**.** Clearly as the abundance of the lay mussels declined most oystercatchers redistributed not to other lays but onto other resources. The impact of the redistribution of these birds on the consumption of these other resources was however very slight as the bulk of the population already exploited these other resources.

7.3 Series 2 simulations

Caldow and others (2004) developed a behaviour based model of oystercatchers foraging on shellfish in the Menai strait. This was used to simulate changes to the way in which the mussels on commercially cultivated lays were managed in order to identify the best ways to minimise losses of harvestable mussels to bird predation and to explore the implications of doing so for the well-being of the oystercatcher population. Caldow and others (2004) discovered that the losses of harvestable mussels could be markedly reduced by altering the stocking density and shore-level of lays at different phases of the cultivation cycle. In the light of that work, this series of simulations was conducted in order to establish the implications for the current overwintering populations of eider ducks and oystercatchers of gross changes to the way in which the current stock of lay mussels (c 10,000 tonnes) is distributed within and between the principal lays of The Wash. These simulations were also conducted to reveal the extent to which such changes to the management of the lay stock might alter the predation pressure exerted by the birds on the lay resource as a whole and upon particular lays. Simulations were conducted not just against the present day background of the alternative shellfish resources to which birds could switch, but assuming another scenario in which the abundance of the *Ensis* stock was assumed to have declined to a low level. This was necessary to establish whether the implications of changes to the distribution of the current lay mussel resources might vary given a change to the other principal resource on which eiders in The Wash appear to depend. Given the history of the *Ensis* population in The Wash, such a decline is quite likely (D. Palmer pers. comm.).

7.3.1 Eiders

Percentage of population supported The model predicted that the further concentration of the existing lay resources (by doubling the numerical density of mussels on each lay while halving its area) would have no detrimental effect on the percentage of the eider population that could be supported, and might indeed improve matters slightly if *Ensis* were scarce. In contrast, removing the best 'hot spots' of high mussel density on the lays, either by spreading the mussels over twice the area on each lay, or by equalising the numerical density of mussels across all lays, is predicted to reduce the percentage of the eider population that can be supported. This is particularly true if *Ensis* stocks are low. These results arise from the fact that eiders are not assumed to exhibit interference competition (see section 3.7.3) such that increasing concentration of the lay mussel resource will not result in any decline in the intake rates achieved by the birds. In contrast, concentration of the existing lay resources, by increasing the numerical density of mussels, will enhance the interference free intake rate that birds can achieve whereas spreading the existing lay resources more widely or at a lower average density will have the opposite effect.

Distribution of predation pressure between alternative shellfish resources Increasing the extent to which the lay mussel resources are concentrated is predicted to increase their profitability to eiders and result in an increase in the losses of lay mussels (660 tonnes v 606 tonnes) and a slight decline in eiders' usage of other resources. In contrast, decreasing the extent to which the lay mussel resources are concentrated is predicted to decrease their profitability to eiders and result in the losses of lay mussels decreasing (398 tonnes v 606

tonnes) and an increase in their usage of other shellfish resources. This spreading out to utilise other shellfish resources is not, however, sufficient to maintain the percentage of the eider population that can be supported. These patterns are more or less the same if the stock of *Ensis* was assumed to have declined to a low level.

Distribution of predation pressure between commercially cultivated lays Increasing the extent to which the lay mussel resources are aggregated is predicted to further enhance the relative profitability of the initially best areas (ie Roger and Toft) to eider ducks and result in increased losses from them. In contrast, reducing the numerical density of mussels by spreading mussels more thinly on all lays is predicted to decrease the predation pressure on the best lays but not to result in any spread of predation to the other lays which retain their relatively poor profitability. However, making the lays more similar to one another by evening out variations in the numerical density of mussels, lay areas and shore height is predicted to even out eider predation pressure too, but at the expense of decreasing the percentage of the eider population that can be supported.

In summary, increasing the extent to which the lay mussel resources are aggregated increases their profitability to eider ducks and results in increased losses from them. Reducing the numerical density of mussels by spreading mussels more thinly on all lays will decrease the predation pressure on the lays, increase the birds' reliance on other resources, and probably result in a decrease in the percentage of the eider population that can be supported. These simulations confirm the findings of Stillman and others (2003) and Caldow and others (2004) that changes to the way in which a given stock of mussels is distributed can have a marked influence on the distribution of predation pressure by a large population of mussel feeding birds, and potentially on the proportion of such a population that can be supported by the resources.

7.3.2 Oystercatchers

Percentage of population supported The percentage of the oystercatcher population that was predicted to be supported was constant irrespective of changes to the way in which the lay mussel stock was distributed and irrespective of the level of the *Ensis* stock (which in any case they are assumed not to eat). This is in contrast to the findings of Stillman and others (2003) who predicted that the overwinter mortality of oystercatchers in The Wash could be dramatically altered by varying the density and shore height at which an additional bed of c 10,000t of mussels was laid. However, the simulations conducted by Stillman and others (2003) mimicked the background cockle and regulated mussel stocks available in the poorest years of the early 1990s. Thus, it is not surprising that, in the absence of any viable alternative stock on which the birds could feed, the precise shore height and density at which the only potentially profitable resource was made available to them made such a pronounced difference. In contrast, the simulations conducted in this series assumed that the cockle and regulated mussel stocks in The Wash were as they are today ie relatively healthy. Under these circumstances, the simulations conducted under series 1 indicated that the percentage of the oystercatcher population that could be supported was unaffected by the complete removal of the mussel lays, never mind modifications to the way in which the existing stock is distributed. It should be remembered however, that the series 1 simulations also indicated that when the stocks of cockles and regulated mussels were set to mimic the very poor

conditions of the early 1990s (scenario 3), the percentage of the oystercatcher population that could be supported was markedly depressed and made worse by the removal of the mussel lays. Thus, had simulations in this series been conducted against this background it is possible that the changes to the distribution of the lay resources would have affected oystercatchers more than the current results indicate. Thus, the current findings probably reflect the relatively healthy stocks of cockles and mussels on the regulated beds and hence the relatively minor use made of the lays by the population of oystercatchers in these conditions. The results of this series of simulations are in accord with the findings of Caldow and others (2004) who noted that many of the modelled changes to the way in which the stock of lay mussels in the Menai strait was distributed, while affecting the birds' predation pressure, had no noticeable effect on their over-winter survival. Again, this reflects the super abundance of the resources available to the oystercatchers in most of the simulations conducted by Caldow and others (2004).

Distribution of predation pressure between alternative shellfish resources Given the relatively minor use of the lay resources by oystercatchers in the model, the lack of any change to their usage of alternative shellfish resources as the distribution of the lay mussels was manipulated is not surprising.

Distribution of predation pressure between commercially cultivated lays Caldow and others (2004) demonstrated that by altering the numerical density of mussels on lays and their shore level relative to one another it was possible to markedly shift oystercatcher predation pressure from one lay to another, and in so doing to reduce losses of ready to harvest mussels. The results of the current study confirm these effects. The principle result is that concentrating the mussel resources reduces the profitability of the best lays to oystercatchers and reduces losses from them whereas spreading the mussels out more thinly increases the profitability of the best lays and results in increased losses from them. These results are in direct contrast to those concerning the effects of manipulating the distribution of lay stocks on eider predation pressure. However, because of the relatively minor predation pressure exerted by oystercatchers in comparison to eiders, the changes to the overall losses from individual lays (and from lays as a whole) mediated by changing the distribution of mussels are driven more by the responses of eider ducks than oystercatchers.

7.4 Series 3 simulations

This series of simulations was conducted in order to establish the maximum size of the eider population that could be supported if wild, native shellfish stocks in The Wash were to attain the highest abundance that might be expected in the future, but in the presence/absence of 'un-natural' shellfish resources ie commercially cultivated lay mussels and non-native *Ensis directus*. Both of these latter resources, being 'un-natural', could 'disappear' and have marked consequences for the eider and oystercatcher populations. The current magnitude of the commercially cultivated mussel stock available to the birds is unprecedented and could be reduced in the future either as a result of protective measures being put in place by the fisherman or a market-led decline in the scale of the industry. *Ensis directus* is a non-native species which has only colonised European waters within the last 30 years or so (Palmer 2003). The population of this species in The Wash exhibits only intermittent episodes of good recruitment and lives for only a short time. This has resulted in large fluctuations in the stock over the years. Such variation is highly likely to continue (D. Palmer pers. comm.). Thus,

there is considerable merit in exploring how the size of the eider population that could be supported in The Wash is likely to vary given the uncertainty over the future of these two stocks of shellfish.

The results of these simulations indicate that in the absence of both commercially cultivated mussel stocks and *Ensis*, the natural stocks of cockles and mussels on the regulated beds, even if ascribed high stock levels, cannot support a population of eider ducks of any significant size without a significant proportion of these being at risk or mortality. This is not to say that a significant number of eider could not be supported by these natural stocks, simply that it could only be the most efficient foragers amongst a much larger population that could be supported. The bulk of the population could not be supported. This is almost certainly a reflection of the relatively poor quality of the regulated mussels and cockles in the model and the overriding importance of prey quality in eider foraging dynamics (Guillemette 1994; Nehls 1995; Bustnes 1998). Mussels from mid-shore wild mussel beds generally have a poor flesh: shell ratio in comparison with mussels from low-shore or subtidal lays (Leopold, Kats & Ens 2001; Hart & Brown 2006; R. Caldow unpubl data) and this is reflected in the model resources. The samples of cockles which were used to characterise the quality of cockles in the model were taken from various locations in The Wash in autumn 2004. In agreement with the views of the industry and ESFJC, expressed in the Appropriate Assessment document (English Nature 2005), they exhibited low flesh content. It is almost certainly this low quality of the natural shellfish resources that limits their ability to support as large a population of eiders as the stock of lay mussels.

The simulations also indicate that even in combination with healthy stocks of mussels on the regulated beds and healthy cockle stocks, a healthy stock of *Ensis* cannot, in the absence of commercially cultivated mussel stocks, support the present peak population of eiders without a significantly greater percentage being at risk. In the absence of commercially cultivated mussel stocks, only a peak population of less than 1,000 birds could be supported without the percentage at risk of not being able to survive the winter exceeding a 'normal' overwinter eider mortality rate of c 5 per cent. This series of simulations also revealed that in the absence of a healthy stock of *Ensis*, the maximum peak population that the lays can support, without the percentage at risk of not being able to survive the winter exceeding a 'normal' overwinter eider mortality rate of c 5 per cent, is less than the current peak population size of c 3,000 birds. Nonetheless, it is the presence today of a large scale commercially cultivated mussel industry in The Wash that, more than any other factor, allows a peak population of in excess of 2,000 eider ducks to be supported. The inability of the current lay stock to support the observed peak population of c 3,000 birds reflects the observation that in the model most of the eider population switched to feeding on *Ensis* at the end of the winter. This occurred in reality at the end of the 2005-2006 winter (Hart & Brown 2006). Hart & Brown (2006) attributed this to the dredging of the mussels on the eiders' preferred lays. However, in the model this switch occurred whether the removal of these mussels by the fishermen was included or not. Other reasons for such dietary switches, which are often observed in other diving ducks (Lovvorn 1989a; Sekiya and others 2000), include: i) the depletion of the birds' preferred resources (mussels in this case) by the birds themselves over the winter, ii) losses of mussels due to other sources of mortality and iii) the over-winter decline in flesh content which occurs in mussels.

Just as the disappearance of large numbers of eiders from the Wadden Sea in the early 1990s may have arisen from the coincidence of low stocks of natural mussels and cockles (Beukema 1993) it may be that the recent increase in the peak population of eiders in The Wash may reflect the coincidence of an abundant stock of lay mussel resources and a peak population of the non-native *Ensis directus*. The model predicts that together these resources have the capacity to support a peak population of between 10,000 and 12,000 eiders without the percentage at risk of not being able to survive the winter exceeding a 'normal' overwinter eider mortality rate of c 5 per cent. These conclusions are unlikely to be significantly affected by the health of the cockle or wild mussel stocks which are, in comparison with lay mussel and *Ensis*, apparently unprofitable and less-preferred resources. Thus, given the data concerning the relative quality of the various shellfish resources available to eiders, it can be concluded that the ability of The Wash to support the current peak population of eiders is determined by the abundance of the 'un-natural' shellfish resources ie commercially cultivated lay mussels and non-native *Ensis directus* rather than the stocks of the wild, native shellfish.

7.5 General discussion

Eider numbers in The Wash have, according to counts conducted under the WeBS scheme, fluctuated greatly on a year-to-year basis over the last 40 years. Although these land-based counts give accurate counts of birds seen, they are limited in seaward extent and are thus unlikely to give an accurate assessment of total numbers. Furthermore, the accuracy of sea duck counts from land is affected by the suitability of viewing conditions, particularly sea state, and by the limited time available to make the lengthy scans of the sea needed to record sea duck numbers accurately (Smith, Hall, Worden, Harrison, Allen, Bradbury, Cranswick, Woodward, Shepherd, Paynter & McGill 2006). Nonetheless, during four successive years in the first half of the 1980s, consistently large numbers of eiders were recorded by the WeBS scheme. For the reasons just discussed, these counts will, if anything have tended to be underestimates. At that time, the commercial cultivation of mussels on lays was far less extensive than today. Given that *Ensis directus* was first identified in European waters in the German Bight in 1979 (Palmer 2003), it is unlikely that there was an abundant stock of this species in The Wash in the early 1980s. In the absence of both of these resources, which the model suggests are of key importance to the current eider population, it is interesting to speculate as to what supported the apparently equally high eider population in the early 1980s.

Historical surveys of the stocks of mussels and cockles in The Wash (Dare and others 2004) reveal that in the late 1970s there was a sequence of moderate and high spatfalls of mussels in The Wash resulting in a period when stocks were assessed as being plentiful. The first full mussel stock survey since 1957 that was conducted in1981 found c18,000t of mussels (Dare and others 2004). In 1982 the Gat beds alone held an estimated 14,000 t. After 1982, mussel stocks showed a rapid decline which, apart from a brief recovery in the late 1980s, continued until c 2000 (Dare and others 2004). A time-series plot of the annual indices of the fishable stock of cockles in The Wash indicates that prior to 2000, the last sequence of high stock index values occurred over three successive years 1982 - 1984. Thus, historical survey data indicate that the last time that the stocks of mussels and cockles in The Wash were healthy simultaneously was in the very early 1980s. This may provide the explanation for the peak in the eider population in The Wash at that time. However, the model predicted that even in the

presence of abundant cockle and regulated mussel stocks, the population of eider that could be supported without a large proportion being 'at risk' was very small in the absence of both commercially cultivated lay mussel and *Ensis* stocks. There are a number of possible explanations for this apparent anomaly.

First, the historical cockle abundance index values cannot be scaled to absolute abundance (Dare and others 2004) and it is thus not possible to determine just how big the cockle stock was in the early 1980s. It is possible (though unlikely) that the total stock was greater than the value that we have assumed to represent a healthy autumn stock (50,000t of both fishable and juvenile cockles). Secondly, it is possible that the stock of cockles in the 1980s was concentrated in a smaller area than today. The results of our simulations suggest that this would have rendered them more profitable as a prey resource. It is known that the numerical density of large cockles is low at present (see below).Thirdly, it is possible that the mussels and particularly the cockles had higher flesh content in the early 1980s than today. It is known that the flesh content of cockles on some beds today is very low (see below). Finally, perhaps there was another as yet unidentified alternative resource which eider ducks exploited in The Wash in the early 1980s. Given these uncertainties, the presence of a large population of eiders in The Wash in the early 1980s, prior to the expansion of the commercial cultivation of mussels on lays and the growth of the *Ensis directus* stock, is not wholly at odds with the results of this study which stresses the importance of these two resources to the current peak eider population.

Guillemette, Ydenberg & Himmelman (1992) stated that "we have no difficulty imagining that starvation could be a major cause of natural mortality in wintering eiders". This arises principally from the fact that eider ducks ingest their prey whole and consequently ingest a large quantity of indigestible (shell) material with every prey item. Guillemette (1994) found that eiders ingested blue mussels twice as fast as they were able to digest them, showing the importance of the digestive constraint. The general problem for these birds is thus not to find food (fast enough) but to locate prey with sufficient quality ie energy density to fulfill the daily energy requirement without exceeding their gut processing capacity. Nehls (1995) noted that the tight energy budget of eiders stresses the importance of mussel quality (shell thickness and flesh content) as a criterion for foraging site and food selection. Nehls (2001) noted that eiders feeding on poor mussels could in principle starve despite having a full stomach. This suggests that in assessing the condition of The Wash, in terms of the size of the eider population that it can support, the key issue is not simply a matter of the numerical density of shellfish stocks or the total live mass tonnage available, but also the quality of the shellfish available ie the flesh content relative to that of the shell. This issue of relative prey quality is probably at the heart of the current conflict between eider ducks and commercial mussel growers in The Wash.

In those years in the late 1990s and early 2000s when eider numbers were (relatively) high, WeBS count data indicate that they were concentrated in the Snettisham sector (in 1996 and 1997) on the east of The Wash and on the north-western side of The Wash ie Wrangle, Friskney & Leverton (in 2000, 2001, 2002 and 2003). These distribution data coincided well with the results of the low-tide survey of bird distribution conducted in the winter of 2002-2003 (Yates, Garbutt, Rispin & Brown 2004) when eiders occurred in highest numbers on the Friskney Flats, Scullridge and Wrangle Flats. Observations during these low tide surveys indicated that the eider pellets/droppings contained cockle fragments (M. Yates pers comm.).

Wrangle, Friskney, Leverton and Snettisham (Stubborn Sand) are areas that consistently support cockle beds, suggesting that in these years eider had been feeding mainly on cockles. However, the recent marked increase in eider numbers on the lays of Roger/Toft, and the results of the aerial surveys of The Wash in 2005-2006 (Smith, Hall, Worden, Harrison, Allen, Bradbury, Cranswick, Woodward, Shepherd, Paynter & McGill 2006), suggest that eider have switched to feeding mainly on mussels. The density of large cockles on the cockle beds is low at present in comparison to 2002 when eiders were apparently feeding primarily on cockles (English Nature 2005). Moreover, the industry and ESFJC have reported that there are some beds of cockles which have recently had very low flesh content, which has been linked to food shortage (English Nature 2005). These factors, in combination with a readily available, abundant and high quality lay mussel resource, almost certainly have precipitated the switch of eider ducks to mussel feeding in recent years.

The fact that eiders in The Wash now concentrate on feeding on commercially cultivated lay mussels (Hart & Brown 2006; Smith, Hall, Worden, Harrison, Allen, Bradbury, Cranswick, Woodward, Shepherd, Paynter & McGill 2006) is entirely consistent with their behaviour in other systems, notably the Wadden Sea. Camphuysen and others (2002) noted that Swennen, Nehls & Laursen (1989) had indicated that eiders in the Wadden Sea had obtained c 20 per cent of their prey from mussel culture lots in the past, but that since the early 1990s the significance of mussel cultures for wintering eiders has increased markedly. This may have been precipitated by a coincidence of low stocks of wild mussels and cockles in 1990/91 resulting in birds wintering in the Dutch Wadden Sea concentrating on the last mussel banks present ie the culture lots, where they were regularly chased away. A significant proportion left the area or died in that case (Beukema 1993). In more recent years in the Dutch Wadden Sea, the vast majority of eiders reside over subtidal cultured mussels if they are available (Leopold, Kats & Ens 2001). Leopold, Kats & Ens (2001) attributed this preference to mussels on culture lots having thinner shells and being less well attached to each other than intertidal ones. Nehls & Ruth (1994) also noted that eiders may concentrate in flocks of several thousands on mussel culture lots in the Wadden Sea and that the utilisation of mussel cultures by eiders relates to the amount and size structure of the mussels found in these places. The proportion of wintering eiders found on or close to culture lots closely follows the proportion of mussels found on the cultures (out of the total stock in the system). In 1991 and 1992 when eider numbers on the cultures were exceptionally high, mussel stocks on the cultures were very high and natural stocks low (Nehls & Ruth 1994). Furthermore, the suitability of mussel beds or cultures for eiders is dependent upon the length distribution of the mussels. The high proportion of eiders found on mussel cultures in 1991 and 1992 coincided with the subtidal mussel stock reaching a length preferred by eiders (30mm - 55mm mostly), in contrast to 1990 when mussels on the cultures were small (8mm - 28mm) and few eiders utilised these places. However, this situation is not consistent over all years. In 1988 and 1989 when the mussels on the cultures were of similar size as in 1991 and 1992, but natural stocks of mussels were higher than during 1991 and 1992, few eiders were seen on mussel cultures (Nehls & Ruth 1994). Thus, the tendency of eider ducks to exploit commercially cultivated mussel resources is influenced by a number of factors including the relative abundance and quality of the resources available to them on the lays and elsewhere. Their heavy utilisation of the lays in The Wash at present is almost certainly a combination of the relatively low numerical density and quality of the natural native shellfish stocks ie cockles and regulated mussels and an abundant stock of high density, high quality, and suitably sized mussel available on the commercially cultivated lays.

Hart & Brown (2006) noted that following the dredging of the Roger Lay in early 2006, the numbers of eiders observed there during high water, and the number observed foraging on or adjacent to the lay during low water, declined. They concluded that many eiders may have exploited food resources outside the lay study area after fishing depletion of the mussel resources. Hart & Brown (2006) noted 1,050 eiders and 1,200 common scoters on Scull ridge where dredge samples revealed an abundance of juvenile razor shells *Ensis* spp. (ESFJC unpublished data). Preliminary runs of the model in which the dredging of the lay mussels was included indicated that eiders would indeed switch to feeding on *Ensis* at this point in the winter. Interestingly, in all subsequent runs of the model in which this late-winter dredging of mussels was not included, eiders were still predicted to switch to a large degree from feeding on mussels to feeding on *Ensis*. This probably reflects the heavy over-winter depletion of the preferred lays by the eiders themselves, coupled with the assumed rate of loss of mussels due to other mortality factors and the over-winter decline in the flesh content of mussels. All of these factors result in the mussel resources becoming steadily less profitable as the winter progresses. This switch to an alternative resource is entirely consistent with the behaviour of many diving ducks. For example, Sekiya and others (2000) noted that both tufted ducks and pochard *Aythya ferina* switch diet in late winter and feed on Manila clams *Ruditapes philippinarum* and Crustacea after the biomass of mussels *Musculista senhousia* had declined in late winter. Lovvorn (1989a) noted that in South Carolina, canvasbacks *Aythya valisineria* exhibit a sequential use of underground tubers of aquatic plants (*Vallisneria americana* and *Potamogeton pectinatus*) and then clams (mostly *Macoma* spp.) as a result of initially high foraging efficiency for tubers, which declines as the tubers are depleted. Leopold, Kats & Ens (2001) noted that in most situations, at least one other prey species (other than mussels) is also important to eiders. In the Wadden Sea, cockles fill this role. When both of these primary species are scarce eiders have been recorded feeding extensively on *Spisula subtruncata* in the Wadden Sea and on the alien shellfish *Ensis directus* (Leopold and others in press). Scheiffarth, Kempf & Potel (2001) noted that the occurrence of shore crabs *Carcinus maenas* in the diet of eiders wintering in the Wadden Sea in 1999/2000 might have indicated a shortage of suitable mussels and cockles in the area. All of these studies indicate that over-wintering populations of diving ducks often cannot rely on one single prey species but need to be able to exploit alternative prey. Indeed it is often the health of these alternative prey resources that may be of overriding importance in determining the consequences of changes to the abundance or availability of the preferred food (Lovvorn 1989a). The results of the model indicate that it is the presence of a large scale commercially cultivated mussel industry in The Wash that, more than any other factor, allows a population of in excess of 2,000 eider ducks to be supported. However, when a large scale of commercial mussel cultivation combines with an abundant stock of *Ensis directus*, as is the case currently in The Wash, it is predicted to be able to support a peak population of eiders far in excess of that currently observed without an atypically high proportion of that population being at risk of mortality. Whether this potential is ever realised will depend upon the continued availability to eiders of a large quantity of high density, high quality lay mussels and the continued existence of a large stock of *Ensis directus*. It is, however, likely that even given the continued presence of such peaks in the abundance of these 'un-natural' resources, that their potential to support such a large peak eider population will not be realised simply due to there not being a sufficient supply of birds to do so.

8. Conclusions

8.1 Current situation

The principal conclusions that can be reached regarding the current distribution of eider ducks (and oystercatchers) within The Wash, their impact on the commercially cultivated mussel stocks and their over winter survival, are as follows:

1. The recent aggregation of a very high proportion of the eider population on the Roger and Toft lays can be explained purely in terms of the high density of high quality shellfish of a suitable size present there in comparison with that available on the other lays and beds of other shellfish species. Eiders are not predicted to utilise any other commercially cultivated or regulated mussel bed to any significant extent.
2. The proportion of the oystercatcher population that exploits the commercially cultivated mussel lays is far smaller than that of eiders. This probably reflects the relatively low position of the lays on the shore, the occurrence of strong interference competition between foraging oystercatchers (but not between eiders), and the comparatively strong pressure on eiders to select lay mussels over all other resources because of their favourable flesh:shell ratio.
3. Over-winter losses of mussels from lays to eiders and oystercatchers are estimated to be around 600 - 650 tonnes and 100- 150 tonnes respectively. In the case of eiders this is entirely from the Roger and Toft lays.
4. As observed in reality, eider ducks are predicted to switch from feeding on lay mussels to feeding on *Ensis* in late winter. This can be explained purely on the basis of the depletion of the lay mussels by the birds themselves, losses of mussels due to other mortality factors (other than harvesting by the birds and fishermen) and the decline in the flesh content of mussels.
5. The percentage of the current peak eider population of 3,000 birds that cannot be supported is predicted to be around 4 per cent. This is in close agreement with independent estimates of the typical overwinter mortality rate of eiders.
6. The percentage of the peak oystercatcher population of 15,000 birds that cannot be supported is predicted to be zero.

8.2 Predicted effects of a decline in the availability/abundance of lay mussels

The principal conclusions that can be reached regarding the likely changes to the distribution of eider ducks (and oystercatchers) within The Wash, their impact on the commercially cultivated mussel stocks and other shellfish resources and their over winter survival in the light of simulated declines in the availability/abundance of lay mussels and other shellfish stocks, are as follows:

7. Provided that the stock of *Ensis* remains healthy, the stock of lay mussels available to eiders could be reduced by up to 50 per cent without any significant effect upon them.

8. If the stock of lay mussels available to eiders is reduced below around 50 per cent of its current value, the percentage of the eider population that could be supported is predicted to decline significantly, even in the presence of a healthy *Ensis* stock.
9. As the abundance of lay mussels on the best lays is reduced, eider predation on the remaining lays will increase and they will switch to alternative shellfish resources. However, this will not be sufficient to ensure that the percentage of the population that can be supported will be maintained
10. In the absence of a healthy stock of *Ensis*, the percentage of the eider population that can be supported is predicted to be far more vulnerable to any loss of access to lay mussel resources.
11. Variation in the abundance of cockles or mussels on the regulated beds was not predicted to significantly alter the effect on eider ducks of changes to the abundance of lay mussels.
12. The well being of the current high population of eiders is dependent upon the continued health of the *Ensis* stock and continued access to a considerable fraction of the existing lay mussel stock.
13. Given most likely future shellfish stock scenarios, the population of oystercatchers, unlike that of eiders is not predicted to be vulnerable to changes to the abundance of the lay mussel resource.
14. Given most likely future scenarios, changes to the abundance of the lay mussel resource did not result in a spreading out of oystercatcher predation pressure on to the remaining lays, or to a noticeable increase in the predation pressure already exerted by the bulk of the population on the other shellfish resources.

8.3 Predicted effects of changes to the distribution of the existing stock of lay mussels

The principal conclusions that can be reached regarding the likely changes to the distribution of eider ducks (and oystercatchers) within The Wash, their impact on the commercially cultivated mussel stocks and other shellfish resources and their over winter survival in the light of simulated changes to the distribution of the existing stock of lay mussels, are as follows:

15. Increasing the extent to which the lay mussel resources are concentrated is predicted to increase the relative profitability of the already best areas to eider ducks and to result in increased losses from them and hence from lays as a whole (660 tonnes v 606 tonnes) and a slight decline in eiders' usage of other resources.
16. Increasing the extent to which the lay mussel resources are concentrated will have no detrimental effect on the percentage of the eider population that can be supported.
17. Decreasing the extent to which the lay mussel resources are concentrated is predicted to decrease the relative profitability of the best areas to eiders, reduce predation pressure on the best lays and result in the losses of lay mussels decreasing (398 tonnes v 606 tonnes) and an increase in their usage of other shellfish resources (especially *Ensis* if present).
18. Evening out variations in the numerical density of mussels between the lays is predicted to even out eider predation pressure between them.
19. Removing the best 'hot spots' of high mussel density on the lays is predicted to reduce the percentage of the eider population that can be supported.

20. The percentage of the oystercatcher population that is supported is predicted to be constant irrespective of changes to the way in which the lay mussel stock is distributed.
21. Changes to the distribution of the lay mussel stock are predicted to have no significant effect on oystercatchers' relative usage of their three principal shellfish resources.
22. In contrast to eiders, increasing the extent to which the lay mussel resources are concentrated is predicted to reduce the profitability of the best lays to oystercatchers and to reduce losses from them. In contrast, spreading the mussels out more thinly increases the profitability of the best lays and results in increased losses from them.
23. Because of the relatively minor predation pressure exerted on the lays by oystercatchers in comparison to eiders, changes to the overall losses from the lays mediated by changing the distribution of mussels are driven more by the responses of eider ducks than oystercatchers.

8.4 The size of the eider and oystercatcher populations that can be supported

The principal conclusions that can be reached regarding the size of the eider and oystercatcher populations that can be supported by the various shellfish resources in The Wash are as follows:

24. The current stocks of wild mussels on regulated beds and cockle stocks are, on their own, sufficient to support the current peak population of 15,000 oystercatchers while maintaining the percentage that cannot be supported at very low values.
25. If the stocks of mussels on the regulated beds and the stocks of cockles return to the low values seen in the early 1990s, the current peak population of 15,000 oystercatchers cannot be maintained while ensuring that the percentage at risk remains at very low values.
26. Current (or greater) stocks of wild mussels on regulated beds and cockle stocks are, on their own, insufficient to support the current peak population of 3,000 eiders while maintaining the percentage of the population that cannot be supported at below 5 per cent. This reflects the relatively poor quality of these natural shellfish resources.
27. A healthy stock of *Ensis* (in combination with current or greater stocks of mussels on the regulated beds and healthy cockle stocks) cannot, in the absence of commercially cultivated mussel stocks, maintain the present peak population of eiders without in excess of 5 per cent being at risk.
28. In the absence of a healthy stock of *Ensis*, the maximum peak population of eiders that the current lay mussel stock can support, without the percentage at risk of not being able to survive the winter exceeding 5 per cent, is less than the current peak population of 3,000 birds.
29. The recent high peak populations of eiders in The Wash probably reflect the coincidence of an unprecedented abundant stock of lay mussel resources and a peak population of the non-native *Ensis directus*. Together, these resources have the capacity to support a peak population of between 10,000 and 12,000 eiders.
30. The ability of The Wash to support the current peak population of eiders is determined by the abundance of the 'un-natural' shellfish resources ie commercially cultivated lay mussels and non-native *Ensis directus* rather than the stocks of the wild, native shellfish.

In summary, the recently observed concentration of the bulk of a large population of over-wintering eider ducks in The Wash on the Roger and Toft lays is replicated by the model. This is a foraging model, and as such the only reason for it to generate an aggregation of birds in these two locations is the presence there of a large stock of suitably sized, high quality mussels growing at a high density. The model predicts that the eiders consume c 600 tonnes of mussels from these two lays. It also predicts that, as observed, the eiders switch in late winter to feed on *Ensis directus*. The model predicts that by exploiting these two resources alone, the current peak population of c 3,000 eider ducks can be supported with only around 4 per cent being at risk of not being supported. This state of affairs depends upon the continued availability of 'hot-spots' of high densities of high quality mussels such as those available on the Roger and Toft lays, and upon a continued presence of a healthy stock of *Ensis directus*. The current stock and distribution of lay mussels, in combination with a healthy stock of *Ensis directus*, has the capacity to support a far larger peak population of eider ducks than has ever been observed in The Wash. However, in the absence of either of these two resources, there is predicted to be a significant increase in the percentage of the current peak population that will be at risk of not being supported. The health of the stocks of mussels on the regulated beds and cockle beds appear to be relatively unimportant in determining the well-being of the eider population in The Wash. The ability of the shellfish resources in The Wash to sustain the current peak population of c 3,00 birds is primarily a result of the coincidence of a large stock of highly aggregated, high quality lay mussels and a healthy stock of *Ensis directus* ie the stocks of the shellfish which are not a 'natural' part of the Wash ecosystem.

9. Bibliography

ASHCROFT, R. (1976) A function of the pair bond in the common eider. *Wildfowl*, 127, 101 - 107.

BAILLIE, S.R. & MILNE, H. (1989) Movements of Eiders Somateria-Mollissima on the East Coast of Britain. *IBIS*, 131, 321-335.

BALL, J.P. (1990). Active diet selection or passive reflection of changing food availability: the underwater foraging behaviour of canvasback ducks. *In: Behavioural mechanisms of food selection.* (ed R.N. Hughes). Springer-Verlag, Berlin.

BALL, J.P. (1994) Prey choice of omnivorous canvasbacks: imperfectly optimal ducks? *OIKOS*, 70, 233-244.

BARRIOS, L. & RODRÍGUEZ, A. (2004) Behavioural and environmental correlates of soaring-bird mortality at on-shore wind turbines. *Journal of Applied Ecology*, 41, 72-81.

BEADMAN, H.A., CALDOW, R.W.G., KAISER, M.J. WILLOWS, R.I. (2003) How to toughen up your mussels: Using mussel shell morphological plasticity to reduce predation losses. *Marine Biology*, 142, 487 - 494.

BEAUCHAMP, G., GUILLEMETTE, M., & YDENBERG, R. (1992) Prey selection while diving by common eiders, *Somateria mollissima*. *Animal Behaviour*, 44, 417-426.

BEUKEMA, J.J. (1992) Expected Changes in the Wadden Sea Benthos in a Warmer World - Lessons from Periods with Mild Winters. *Netherlands Journal of Sea Research*, 30, 73-79.

BEUKEMA, J.J. (1993) Increased Mortality in Alternative Bivalve Prey During a Period When the Tidal Flats of the Dutch Wadden Sea Were Devoid of Mussels. *Netherlands Journal of Sea Research*, 31, 395-406.

BEUKEMA, J.J. & CADEE, G.C. (1996) Consequences of the sudden removal of nearly all mussels and cockles from the Dutch Wadden sea. *Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I*, 17, 279-289.

BEVAN, R.M. & BUTLER, P.J. (1989) Oxygen-Consumption During Voluntary Diving in the Tufted Duck, Aythya-Fuligula, Acclimated to Summer and Winter Temperatures. *Journal of Physiology-London*, 418, P132-P132.

BEVAN, R.M. & BUTLER, P.J. (1992) Cardiac output and blood flow distribution during swimming and voluntary diving of the tufted duck *Aythya fuligula*. *Journal of Experimental Biology*, 168, 199-217.

BEVAN, R.M. & BUTLER, P.J. (1992) The effects of temperature on the oxygen consumption, heart rate and deep body temperature during diving in the tufted duck *Aythya fuligula*. *Journal of Experimental Biology*, 163, 139-151.

BEVAN, R.M., KEIJER, E., & BUTLER, P.J. (1992) A method for controlling the feeding behaviour of aquatic birds: heart rate and oxygen consumption during dives of different duration. *Journal of Experimental Biology*, 162.

BEVAN, R.M., SPEAKMAN, J.R., & BUTLER, P.J. (1995) Daily Energy-Expenditure of Tufted Ducks - a Comparison between Indirect Calorimetry, Doubly Labeled Water and Heart-Rate. *Functional Ecology*, 9, 40-47.

BLIX, A.S. & FROM, S.H. (1971) Lactate Dehydrogenase in Diving Animals - Comparative Study with Special Reference to Eider (Somateria-Mollissima). *Comparative Biochemistry and Physiology*, 40, 579-&.
BLIX, A.S., MESSELT, E.B., & FROM, S.H. (1973) Lactate-Dehydrogenase in Eider - Unusual Pattern. *Comparative Biochemistry and Physiology*, 44, 625-&.
BORDAGE, D., and others (1998) Use of ratio estimators to estimate the size of common eider populations in winter. *Journal of Wildlife Management*, 62, 185-192.
BOURNE, N. (1984). Clam predation by Scoter ducks in the Strait of Georgia, British Columbia, Canada. Department of fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, British Columbia, British Columbia, Canada.
BRÄGER, S., MEIßNER, J., & THIEL, M. (1995) Temporal and spatial abundance of wintering common Eider *Somateria mollissima*, Long-tailed Duck *Clangula hyemalis*, and Common scoter *Melanitta nigra* in shallow water areas of the southwestern Baltic Sea. *Ornis Fennica*, 72, 19-28.
BREGNBALLE, T., and others (1991) Population processes in the common eider *Somateria mollissima* (eds H. Noer & G. nehls), Vol. 16, pp. 74. Ministry of Environment, Kalø, Denmark.
BUMP, J.K. & LOVVORN, J.R. (2004) Effects of lead structure in Bering Sea pack ice on the flight costs of wintering spectacled eiders. *Journal of Marine Systems*, 50, 113-139.
BUSTNES, J.O. (1998) Selection of blue mussels, *Mytilus edulis,* by common eiders, *Somateria mollissima*, by size in relation to shell content. *Canadian Journal of Ecology*, 76, 1787-1790.
BUSTNES, J.O., and others (2000) The diet of Steller's Eiders wintering in Varangerfjord, northern Norway. *Wilson Bulletin*, 112, 8-13.
BUSTNES, J.O. & ERIKSTAD, K.E. (1988) The Diets of Sympatric Wintering Populations of Common Eider Somateria-Mollissima and King Eider S-Spectabilis in Northern Norway. *Ornis Fennica*, 65, 163-167.
BUSTNES, J.O. & ERIKSTAD, K.E. (1990) Size selection of common mussels, *Mytilus edulis*, by common eiders, *Somateria mollissima*: energy maximization or shell weight minimization? *Canadian Journal of Zoology*, 68, 2280-2283.
BUSTNES, J.O., ERIKSTAD, K.E., & BJORN, T.H. (2002) Body condition and brood abandonment in common eiders breeding in the high Arctic. *Waterbirds*, 25, 63-66.
BUSTNES, J.O. & GALAKTIONOV, K.V. (2004) Evidence of a state-dependent trade-off between energy intake and parasite avoidance in Steller's eiders. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 82, 1566-1571.
BUSTNES, J.O. & LONNE, O.J. (1997) Habitat partitioning among sympatric wintering Common Eiders Somateria mollissima and King Eiders Somateria spectabilis. *IBIS*, 139, 549-554.
BUSTNES, J.O. & SYSTAD, G.H. (2001) Comparative feeding ecology of Steller's Eider and long-tailed ducks in winter. *Waterbirds*, 24, 407-412.
BUSTNES, J.O. & SYSTAD, G.H. (2001) Habitat use by wintering Steller's Eiders Polysticta stelleri in northern Norway. *Ardea*, 89, 267-274.
BUTLER, P.J. (2000) Energetic costs of surface swimming and diving of birds. *Physiological and Biochemical Zoology*, 73, 699-705.

BUTLER, P.J. & WOAKES, A.J. (1979) Changes in heart rate and respiratory frequency during natural behaviour of ducks, with particular reference to diving. *Journal of Experimental Biology*, 79, 283-300.
CABANAC, A.J. (2003) Physical condition of an animal, using as an example the common elder, Somateria mollissima. *Canadian Field-Naturalist*, 117, 230-235.
CALDOW, R.W.G., GOSS-CUSTARD, J.D., STILLMAN, R.A., DURELL, S.E.A.LE.V.DIT., SWINFEN, R., BREGNBALLE, T. (1999) Individual variation in the competitive ability of interference prone foragers: the relative importance of foraging efficiency and susceptibility to interference. *Journal of Animal Ecology*, 68, 869 - 878.
CALDOW, R.W.G., MCGRORTY, S., STILLMAN, R.A., GOSS-CUSTARD, J.D., DURELL, S.E.A. LE V. DIT., WEST, A.D., BEADMAN, H.A., KAISER, M.J., MOULD, K. & WILSON, A. (2004) A behaviour-based modelling approach to reducing shorebird-shellfish conflicts. *Ecological Applications*, 14, 1411 - 1427.
CAMPBELL, L.H. (1978) Diurnal and tidal behaviour patterns of eiders wintering at leith. *Wildfowl*, 29, 147 - 152.
CAMPHUYSEN, C.J. (2001) Eider mortality in the Dutch Wadden Sea, winter 1999/2000. *Wadden Sea Newsletter 2001*, 1, 4 - 5.
CAMPHUYSEN, C.J., and others (2002) Mass mortality of common eiders (Somateria mollissima) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. *Biological Conservation*, 106, 303-317.
CANTIN, M., BÉDARD, J., & MILNE, H. (1974) The food and feeding of common eiders in the St. Lawrence estuary in summer. *Canadian Journal of Ecology*, 52, 319-334.
CARBONE, C. (1995) Guidelines for esimating the feeding performance of diving birds. *Wildfowl*, 46, 119-128.
CARBONE, C., DE LEEUW, J.J., & HOUSTON, A.I. (1996) Adjustments in the diving time budgets of tufted duck and pochard: is there evidence for a mix of metabolic pathways? *Animal Behaviour*, 51, 1257-1268.
CARBONE, C. & HOUSTON, A.I. (1994) Patterns in the diving behaviour of the pochard, *Aytha ferina*: a test of an optimality model. *Animal Behaviour*, 48, 457-465.
CARBONE, C. & HOUSTON, A.I. (1996) The optimal allocation of time over the dive-cycle: an approach based on aerobic and anaerobic respiration. *Animal Behaviour*, 51, 1247-1255.
CHRISTENSEN, T.K. (2000) Female pre-nesting foraging and male vigilance in common eider *Somateria mollissima*. *Bird Study*, 47, 311 - 319.
CHRISTENSEN, T.K., and others (2003). Visual and radar observations of birds in relation to collision risk at the Horns Rev offshore wind farm. National Environmental Research Institute, Ministry of the Environment, Denmark.
COAD, P., & SHEPHERD, N. (2005). Cockle survey - Heacham June 2005. Ecomaris Ltd., Huntigdon.
COULSON, J.C. (1984) The population dynamics of the Eider Duck *Somateria mollissima* and evidence of extensive non-breeding by adult ducks. *IBIS*, 126, 525-543.

CRAMP, S. & SIMMONS, K.E.L. (1977) *Handbook of the Birds of Europe and the Middle East and North Africa. The birds of the Western Palearctic*, Oxford University Press.
CRISCUOLO, F., GAUTHIER-CLERC, M., GABRIELSEN, G.W. & LE MAHO, Y. (2000) Recess behaviour of the incubating comon eider *Somateria mollissima*. *Polar Biology*, 23, 571 - 574.
DARE P.J., B., M.C., WALKER, P., BANNISTER, R.C.A. (2004). Historical and current status of cockle and mussel stocks in The Wash. Centre for Environment, Fisheries and Aquaculture Science, Lowestoft.
DAUVIN, J.-C., JONCOURT, M. (1989) Energy values of marine benthic invertebrates from the western English Channel. *Journal of the Marine Biological Association (U.K.)*, 69, 589 - 595.
DE LEEUW, J.J. (1997) *Demanding divers. Ecological energetics of food exploitation by diving ducks*. PhD, Rijksuniversiteit Groningen, Groningen.
DEGRAER, S., and others (1999) The macrozoobenthos of an important wintering area of the common scoter *(Melanitta nigra)*. *Journal of the Marine Biological Association (U.K.)*, 79, 243-251.
DEKKER, R. (2001) Food situation for common eiders in the western Dutch Wadden Sea in 1999-2000 estimated on long-term macrobenthos monitoring data. *Wadden Sea Newsletter 2001*, 1, 32 - 34.
DEWAR, J.M. (1924) *The bird as a diver, A contribution to the natural history of diving birds*, H. F. & G. Witherby.
DRAULANS, D. (1982) Foraging and size selection of mussels by the tufted duck, *Aythya fuligula*. *Journal of Animal Ecology*, 51, 943-956.
DRAULANS, D. (1984) Sub-optimal mussel selection by tufted ducks *Aythya fuligula:* test of a hypothesis. *Animal Behaviour*, 32, 1192-1196.
DRAULANS, D. (1987) Do tufted Duck and Pochard select between differently sized mussels in a similar way? *Wildfowl*, 38, 49-54.
DRENT, R.H.D., S. (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea*, 68, 225 - 252.
DUNTHORN, A.A. (1971) Predation of Cultivated Mussels by Eiders. *Bird Study*, 18, 107-&.
DURANT, D., and others (2003) The functional response in three species of herbivorous Anatidae: effects of sward height, body mass and bill size. *Journal of Animal Ecology*, 72, 220-231.
DURELL, S.E.A.L.V.D., ATKINSON, P.W. (2004) Differential distribution of Oystercatchers *Haematopus ostralegus* overwintering on the Wash, east England. *Bird Study*, 51, 76 - 82.
DURELL, S.E.A.L.V.D., STILLMAN, R.A., TRIPLET, P., AULERT, C., ONO DIT BIOT, D., BOUCHET, A., DUHAMEL, S., MAYOT, S. & GOSS-CUSTARD, J.D. (2005) Modelling the efficacy of proposed mitigation areas for shorebirds: a case study on the Seine estuary, France. *Biological Conservation*, 123, 67 - 77.
DURELL, S.E.A.L.V.D., STILLMAN, R.A., CALDOW, R.W.G., MCGRORTY, S., WEST, A.D. & HUMPHREYS, J. (2006) Modelling the effect of environmental change on shorebirds: a case study on Poole Harbour, UK. *Biological Conservation*, 131, 459-473.
DURINCK, J., and others (1993) Diet of the Common Scoter *Melanitta nigra* and Velvet Scoter *Melanitta fusca* wintering in the North Sea. *Ornis Fennica*, 70, 215-218.

ENGLISHNATURE (2005). Application to use non-lethal electronic bird-scaring devices on RG1 and TO3a mussel lays in The Wash. Record of Appropriate Assessment under Regulation 48 of the *Conservation (Natural Habitats &c.) Regulations* 1994. English Nature.

EVANS, D.M. & DAY, K.R. (2001) Does shooting disturbance affect diving ducks wintering on large shallow lakes? A case study on Lough Neagh, Northern Ireland. *Biological Conservation*, 98, 315-323.

EXO, K. & HÜPPOP (2002) Offshore - Windenergieanlagen und Vögel. *Jber. Institut Vogelforschung 5*.

FERNS, P.N. (1984) Birds of the Bristol Channel and Severn Estuary. *Marine Pollution Bulletin*, 15, 76-81.

FLEET, D.M. (2001) Numbers of common eiders beached on the German North Sea coast during the mass mortality in the winter of 1999/2000. *Wadden Sea Newsletter 2001*, 1, 6 - 7.

FLINT, P.L., and others (2000) Late Summer Survival of Adult Female and Juvenile Spectacled Eiders on the Yukon-Kuskokwim Delta, Alaska. *Waterbirds*, 23, 292-297.

FLINT, P.L., and others (2000) Annual survival and site fidelity of Steller's eiders molting along the Alaska Peninsula. *Journal of Wildlife Management*, 64, 261-268.

FOX, A.D. (2003) Diet and habitat use of Scoters in the Western Palearctic - a brief overview. *Wildfowl*, 54, 163-182.

FOX, A.D. & MITCHELL, C. (1997) Spring habitat use and feeding behaviour of Steller's Eider Polysticta stelleri in Varangerfjord, northern Norway. *IBIS*, 139, 542-548.

FOX, A.D., PETERSEN, A., & FREDERIKSEN, M. (2003) Annual survival and site-fidelity of breeding female Common Scoter *Melanitta nigra* at Mývatn, Iceland, 1925-58. In British Ornithologists' union, pp. E94-E96. Ibis.

FRITZ, H., DURANT, D., & GUILLEMAIN, M. (2001) Shape and sources of variations of the functional response of wildfowl: an experiment with Mallards (Anas platyrhynchos.). *OIKOS*, 93, 488-496.

GARDARSSON, A. & EINARSSON, A. (1994) Responses of breeding duck populations to changes in food supply. *Hydrobiologia*, 279/280, 15-27.

GARTHE, S. & HUPPOP, O. (2004) Scaling possible adverse effects of marine wind farms on seabirds: developing and applying a vulnerability index. *Journal of Applied Ecology*, 41, 724-734.

GILES, N. (1989) Experiments on substrate choice and feeding efficiency of downy Tufted ducklings. *Wildfowl*, 40, 74-79.

GILES, N. (1990) Effects of increasing larval chironomid densities on the underwater feeding success of downy Tufted ducklings *Aythya fuligula*. *Wildfowl*, 41, 99-106.

GORMAN, M.L.M., H. (1971) Seasonal changes in the adrenal steroid tissue of the common eider *Somateria mollissima* and its relation to organic metabolism in normal and oil-polluted birds. *IBIS*, 113, 218 - 228.

GOSS-CUSTARD, J.D., DURELL, S.E.A.LE.V.DIT. (1987) Age-related effects in oystercatchers *Haematopus ostralegus*, feeding on mussels *Mytilus edulis*, I. Foraging efficiency and interference. *Journal of Animal Ecology*, 56, 521 - 536.

GOSS-CUSTARD, J.D., CALDOW, R.W.G., CLARKE, R.T., WEST, A.D. (1995b) Deriving population parameters from individual variations in foraging

behaviuor: II. Model tests and population parameters. *Journal of Animal Ecology*, 64, 277-289.
GOSS-CUSTARD, J.D., SUTHERLAND, W.J. (1997). Individual behaviour, populations and conservation. *In: Behavioural Ecology. An Evolutionary Approach* (ed J.R. Krebs, Davies, N.B.), pp. 373 - 395. Blackwell Science Ltd., Oxford.
GOSS-CUSTARD, J.D., BURTON, N.H.K., CLARK, N.A., FERNS, P.N., MCGRORTY, S., READING, C.J., REHFISCH, M.M., STILLMAN, R.A., TOWNEND, I., WEST, A.D. & WORRALL, D.H. (2006a) Test of a behaviour-based individual-based model: response of shorebird mortality to habitat loss. *Ecological Applications*, 16, 2215 - 2222.
GOSS-CUSTARD, J.D., WEST. A.D., YATES, M.G., CALDOW, R.W.G., STILLMAN, R.A., BARDSLEY, L. (2006b) Intake rates and the functional response in shorebirds (*Charadriiformes*) eating macro-invertebrates. *Biological Reviews*, 81, 1 - 29.
GOSS-CUSTARD, J.D., STILLMAN, R.A. (in press) Individual-based models and the management of shorebird populations. *Natural Resource Modelling*.
GOSS-CUSTARD, J.D., and others (1995a) Deriving population parameters from individual variations in foraging behaviour. I. Empirical game theory distribution model of oystercatchers *Haematopus ostralegus* feeding on mussels *Mytelus edulis*. *Journal of Animal Ecology*, 64, 265-276.
GOUDIE, R.I. (1984) *Comparative ecology of common eiders, black scoters, oldsquaws and harlequin ducks wintering in southeastern Newfoundland.* M.Sc., University of Western Ontario, London, Ontario.
GOUDIE, R.I. & ANKNEY, C.D. (1986) Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. *Ecology*, 67, 1475-1482.
GREEN, J.A., and others (2005) Do seasonal changes in metabolic rate facilitate changes in diving behaviour? *Journal of Experimental Biology*, 208, 2581-2593.
GREMILLET, D. & WILSON, R.P. (1999) A life in the fast lane: energetics and foraging strategies of the great cormorant. *Behavioral Ecology*, 10, 516-524.
GUILLEMETTE, M. (1994) Digestive-Rate Constraint in Wintering Common-Eiders (Somateria-Mollissima) - Implications for Flying Capabilities. *Auk*, 111, 900-909.
GUILLEMETTE, M. (1998) The effect of time and digestion constraints in Common Eiders while feeding and diving over Blue Mussel beds. *Functional Ecology*, 12, 123-131.
GUILLEMETTE, M. (2001) Foraging before spring migration and before breeding in Common Eiders: Does hyperphagia occur? *Condor*, 103, 633-638.
GUILLEMETTE, M. & HIMMELMAN, J.H. (1996) Distribution of wintering common eiders over mussel beds: Does the ideal free distribution apply? *OIKOS*, 76, 435-442.
GUILLEMETTE, M., and others (1993) Habitat Selection by Common Eiders in Winter and Its Interaction with Flock Size. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 71, 1259-1266.
GUILLEMETTE, M. & LARSEN, J.K. (2002) Postdevelopment experiments to detect anthropogenic disturbances: the case of sea ducks and wind parks. *Ecological Applications*, 12, 868-877.

GUILLEMETTE, M., REED, A., & HIMMELMAN, J.H. (1996) Availability and consumption of food by common eiders wintering in the Gulf of St. Lawrence: evidence of prey depletion. *Canadian Journal of Zoology*, 74, 32-38.
GUILLEMETTE, M., and others (2004) The effect of depth on the diving behaviour of common eiders. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 82, 1818-1826.
GUILLEMETTE, M., YDENBERG, R.C., & HIMMELMAN, J.H. (1992) The role of energy intake rate in prey and habitat selection of common eiders *Somateria mollissima* in winter: a risk sensitive interpretation. *Journal of Animal Ecology*, 61, 599-610.
HALSEY, L., WOAKES, A., & BUTLER, P. (2003) Testing optimal foraging models for air-breathing divers. *Animal Behaviour*, 65, 641-653.
HAMILTON, D.J. (2000) Direct and indirect effects of predation by Common Eiders and abiotic disturbance in an intertidal community. *Ecological Monographs*, 70, 21-43.
HAMILTON, D.J., ANKNEY, C.D., & BAILEY, R.C. (1994) Predation of Zebra Mussels by Diving Ducks - an Exclosure Study. *Ecology*, 75, 521-531.
HAMILTON, D.J. & NUDDS, T.D. (2003) Effects of predation by common eiders (Somateria mollissima) in an intertidal rockweed bed relative to an adjacent mussel bed. *Marine Biology*, 142, 1-12.
HAMILTON, D.J., NUDDS, T.D., & NEATE, J. (1999) Size-selective predation of Blue Mussels *Mytilus Edulis* by common eiders *Somateria Mollissima* under controlled field conditions. *The Auk*, 116, 403-416.
HANCOCK, D.A. (1970) The role of predators and parasites in a fishery for the mollusc *cardium edule* L. Dynamics of populations. In Proceedings of the Advanced Study Institute, Oosterbeek (ed P.J. Den Boer, Gradwell, G.R.). Centre for Agricultural Publishing and Documentation, Wageningen, Netherlands.
HANSSEN, S.A., and others (2003) Costs of parasites in common eiders: effects of antiparasite treatment. *OIKOS*, 100, 105-111.
HARIO, M. & OST, M. (2002) Does heavy investment in foraging implicate low food acquisition for female Common Eiders Somateria mollissima? *Ornis Fennica*, 79, 111-120.
HART, J., BROWN, S. (2006). Detering eider predation of commercial mussel leys in The Wash estuary: the effectiveness of non-lethal scaring devices. Central Science Laboratory Bird Management Unit, York.
HAWKINS, P.A.J., and others (2000) Estimation of the rate of oxygen consumption of the common eider duck (Somateria mollissima), with some measurements of heart rate during voluntary dives. *Journal of Experimental Biology*, 203, 2819-2832.
HEPP, G.R., HAIR, J.D. (1984) Dominance in wintering waterfowl (Anatini): effects on distribution of sexes. *The Condor*, 86, 251 - 257.
HILGERLOH, G. (1997) Predation by birds on blue mussel Mytilus edulis beds of the tidal flats of Spiekeroog (southern North Sea). *Marine Ecology-Progress Series*, 146, 61-72.
HILGERLOH, G. & PFEIFER, D. (2002) Size selection and competition for mussels Mytilus edulis, by oystercatchers, Haematopus ostralegus, herring gulls, Larus argentatus, and common eiders, Somateria mollissima. *Ophelia*, 56, 43-53.
HOHMAN, W.L. (1993) Body composition of wintering Canvasbacks in Louisiana: dominance and survival implications. *The Condor*, 95, 377-387.

HORWOOD, J.W., GOSS-CUSTARD, J.D. (1977) Predation by the oystercatcher, *Haematopus ostralegus* (L.), in relation to the cockle, *Cerastoderma edule* (L.), fishery in the Burry Inlet, South Wales. *Journal of Applied Ecology*, 14, 139 - 158.

HULSCHER, J.B. (1989) Mortality and survival of oystercatchers during severe winter conditions. *Limosa*, 62, 177 - 181.

HULSCHER, J.B. (1990) Survival of oystercatchers during hard winter weather. *Ring*, 13, 167 - 172.

ITAMIES, J., VALTONEN, E.T., & FAGERHOLM, H.P. (1980) Polymorphus-Minutus (Acanthocephala) Infestation in Eiders and Its Role as a Possible Cause of Death. *Annales Zoologici Fennici*, 17, 285-289.

JENSSEN, B.M., EKKER, M., & BECH, C. (1989) Thermoregulation in Winter-Acclimatized Common Eiders (Somateria-Mollissima) in Air and Water. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 67, 669-673.

JESSOP, R.W., & GRAVES, K.M. (2005). Eastern Sea Fisheries Joint Committee Research Report 2005. Eastern Sea Fisheries Joint Committee.

JORDE, D.G. & OWEN, R.B. (1988) Efficiency of nutrient use by American black ducks wintering in Maine. *Journal of Wildlife Management*, 52, 209-214.

KAHLERT, J., DESHOLM, M., & CLAUSAGER, I. (2004). Investigations of migratory birds during operation of Nysted offshore wind farm at Rødsand: Preliminary analysis of data from spring 2004. National Environmental Research Institute. Ministry of the Environment, Denmark.

KAHLERT, J., and others (2003). Investigations of birds during construction and operation of Nysted offshore wind farm at Rødsand. National Environmental Research Institute. Ministry of the Environment, Denmark.

KAISER, M.J., CALDOW, R.W.G., SUTHERLAND, W.J., ELLIOT, A., GALANIDI, M., REES, E.I.S., STILLMAN, R.A., SHOWLER, D. (2005). Predicting the displacement of common scoter *Melanitta nigra* from benthic feeding areas due to offshore windfarms. Crown Estate Commission.

KASELOO, P.A. & LOVVORN, J.R. (2003) Heat increment of feeding and thermal substitution in mallard ducks feeding voluntarily on grain. *Journal of Comparative Physiology B*, 173, 207-213.

KENDEIGH, S.C., DOL'NIK, V.R., & GAVRILOV, V.M. (1977). Avian energetics. *In: Granivorous birds in tiosystems* (eds J. Pinowski & S.C. Kendeigh), pp. 126-425. Cambridge City Press, Cambridge.

KERSTEN, M., VISSER, W. (1996) The rate of food processing in the oystercatcher: food intake and energy expenditure constrained by a digestive bottleneck. *Functional Ecology*, 10, 440 - 448.

KERSTEN, M., PIERSMA, T. (1997) High levels of energy expenditure in shorebirds:metabolic adaptations to an energetically expensive way of life. *Ardea*, 75, 175 - 187.

KIRBY, J.S., EVANS, R.J., & FOX, A.D. (1993) Wintering seaducks in Britain and Ireland: populations, threats, conservation and research priorities. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 3, 105-137.

KOFFIJBERG, K., BERREVOETS, C. & WITTE, R. (2001) Numbers and distribution of wintering common eiders in the Dutch Wadden Sea in 2000. *Wadden Sea Newsletter 2001*, 1, 8 - 10.

KRAMER, D.L. (1988) The behavioural ecology of air breathing by aquatic animals. *Canadian Journal of Zoology*, 66, 89-94.

KREMENTZ, D.G., HINES, J.E., & CAITHAMER, D.F. (1996) Survival and recovery rates of American eiders in eastern North America. *Journal of Wildlife Management*, 60, 855-862.
LARSEN, J.K. & GUILLEMETTE, M. (2000) Influence of annual variation in food supply on abundance of wintering common elders Somateria mollissima. *Marine Ecology-Progress Series*, 201, 301-309.
LAUBHAN, M.K. & METZNER, K.A. (1999) Distribution and diurnal behavior of Steller's Eiders wintering on the Alaska Peninsula. *Condor*, 101, 694-698.
LEOPOLD, M.E.A. (1995) Common scoters *Melanitta nigra* in the Netherlands. *Limosa*, 68, 49-64.
LEOPOLD, M.F., KATS, R.K.H. & ENS, B.J. (2001) Diet (preferences) of common eiders *Somateria mollissima*. *Wadden Sea Newsletter 2001*, 1, 25 - 31.
LEOPOLD, M.F. (2002) Eiders Somateria mollissima scavenging behind a lugworm boat. *Journal of Sea Research*, 47, 75-82.
LEOPOLD, M.F., SPANNENBURG, P.C., VERDAAT, H.J.P., KATS, R.K.H. (in press) Identification and size estimation of *Spisula subtruncata* and *Ensis americanus* shell fragments in stomachs and faeces of common eiders *Somateria mollissima* and common scoters *Melanitta nigra*. *Atlantic Seabirds*.
LEWIS, T.L., and others (2005) Nocturnal foraging behavior of wintering surf scoters and White-winged Scoters. *Condor*, 107, 637-647.
LOVVORN, J.R. (1989a) Distributional responses of canvasback ducks to weather and habitat change. *Journal of Applied Ecology*, 26, 113-130.
LOVVORN, J.R. (1989b) Food Defendability and Antipredator Tactics - Implications for Dominance and Pairing in Canvasbacks. *Condor*, 91, 826-836.
LOVVORN, J.R. (1994) Biomechanics and foraging profitability: an approach to assessing trophic needs and impacts of diving ducks. *Hydrobiologia*, 279/280, 223-233.
LOVVORN, J.R. & GILLINGHAM, M.P. (1996) Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. *Ecology*, 77, 435-451.
LOVVORN, J.R. & JONES, D.R. (1991) Body mass, volume and bouyancy of some aquatic birds and their relation to locomotor strategies. *Canadian Journal of Zoology*, 69, 2888-2892.
LOVVORN, J.R. & JONES, D.R. (1991) Effects of body size, body fat and change in pressure with depth on bouyancy and costs of diving in ducks. *Canadian Journal of Zoology*, 69, 2879-2887.
LOVVORN, J.R., JONES, D.R., & BLAKE, R.W. (1991) Mechanics of underwater locomotion in diving ducks: drag, bouyancy and acceleration in a size gradient of species. *Journal of Experimental Biology*, 159, 89-108.
LOVVORN, J.R., and others (2003) Diet and body condition of spectacled elders wintering in pack ice of the Bering Sea. *Polar Biology*, 26, 259-267.
MARSDEN, S.J. (2000) Impact of disturbance on waterfowl wintering in a UK dockland redevelopment area. *Environmental Management*, 26, 207-213.
MEISSNER, J. & BRAGER, S. (1990) The feeding ecology of wintering eiders *Somateria Mollissima* and common scoters *Melanitta nigra* on the Baltic Sea coast of Schleswigholstein, Frg. *Wader Study Group Bulletin*, 58, 10-12.
MIKOLA, J., and others (1992) The effects of disturbance caused by boating on survival and behaviour of velvet scoter *Melanitta fusca* ducklings. *Biological Conservation*, 67, 119-124.

MILNE, H. (1974) Breeding numbers and reproductive rate of Eiders at the Sands of Forvie National Nature Reserve, Scotland. *IBIS*, 116, 135-154.
MILNE, H. (1976) Body weight and carcass composition of the common eider. *Wildfowl*, 27, 115 - 122.
MITCHELL, C. (1992) Water depth predicts redhead distribution in the lower Laguna Madre, Texas. *Wildlife Society Bulletin*, 20, 420-424.
MORI, Y. & BOYD, I.L. (2004) The behavioural basis for nonlinear functional responses and optimal foraging in Antarctic fur seals. *Ecology*, 85, 398-410.
MUDGE, G.P., ALLEN, D.S. (1980) Wintering seaducks in the Moray and Dornoch Firths. *Wildfowl*, 31, 123 - 130.
NEHLS, G. (1989) Occurrence and Food-Consumption of the Common Eider, Somateria-Mollissima, in the Wadden Sea of Schleswig-Holstein. *Helgolander Meeresuntersuchungen*, 43, 385-393.
NEHLS, G. (1995) *Strategien der Ernahrung und ihre Bedeutung fur Energiehaushalt und Okologie der Eiderente (Somateria mollissima (L., 1758))*. Universitat Kiel, Kiel.
NEHLS, G., HERTZLER, I. & SCHEIFFARTH, G. (1997) Stable mussel *Mytilus edulis* beds in the wadden Sea - They're just for the birds. *Helgolander Meeresunters*, 51, 361 - 372.
NEHLS, G. (2001) Food Selection by Eiders - Why Quality Matters. *Wadden Sea Newsletter 2001*, 1, 39 - 41.
NEHLS, G. & KETZENBERG, C. (2002) Do common eiders *Somateria Mollissima* exhaust their food resources? A study on the natural mussel *Mytilus Edulis* beds in the Wadden Sea. *Danish Review of Game biology*, 16, 47-61.
NEHLS, G. & RUTH, M. (1994) Elders, Mussels, and Fisheries in the Wadden Sea - Continuous Conflicts or Relaxed Relations. *Ophelia*, 263-278.
NEHLS, G. & THIEL, M. (1993) Large-Scale Distribution Patterns of the Mussel Mytilus-Edulis in the Wadden Sea of Schleswig-Holstein - Do Storms Structure the Ecosystem. *Netherlands Journal of Sea Research*, 31, 181-187.
NILSSON, L. (1972) Habitat selection, food choice and feeding habits of diving ducks in coastal waters of South Sweden during the non-breeding season. *Ornis Scandinavia*, 3, 55-78.
NYSTROM, K.G.K., PEHRSSON, O., BROMAN, D. (1991) Food of juvenile common eiders (*Somateria mollissima*) in areas of high and low salinity. *The Auk*, 108, 250 - 256.
OKA, N., and others (1999) Habitat selection by wintering tufted ducks with special reference to their digestive organ and to possible segregation between neighboring populations. *Ecological Research*, 14, 303-315.
OST, M.K., M. (1999) Parental care influences the feeding behaviour of female eiders *Somateria mollissima*. *Annales Zoologici Fennici*, 36, 195 - 204.
OWEN, M., ATKINSON-WELLES, & SALMON (1986). Principal Species (common Scoter, Velvet Scoter). *In: Wildfowl in Great Britain (2nd edition)*. Cambridge University Press.
PALMER, D. (2003) The introduced razor fish *Ensis directus* in The Wash and north Norfolk. *Shellfish News*, 16, 13 - 15.
PARKES, R., HALSEY, L.G., WOAKES, A.J., HOLDER, R.L. & BUTLER, P.J. (2002) Oxygen uptake during post-dive recovery in a diving bird *Aythya fuligula*: implications for optimal foraging birds. *Journal of Experimental Biology*, 205, 3945 - 3954.

PARTRIDGE, J.K. (1989) Lower Lough Erne's Common Scoters. *RSPB Annual Review*, 25-27.
PEDROLI, J. (1982) Activity and time budget of Tufted Ducks on Swiss lakes during winter. *Wildfowl*, 33, 105-112.
PETERSEN, I.K. (2004). Investigation of birds during the operational phase of the Nysted offshore wind farm. Preliminary notes on the issue of potential habitat loss. National Environmental Research Institute.
PETERSEN, I.K., CLAUSAGER, I., & CHRISTENSEN, T.K. (2004). Bird numbers and distribution in the Horns Rev offshore wind farm area. National Environment Research Institute. Ministry of the Environment, Denmark.
PETERSEN, M.R. & DOUGLAS, D.C. (2004) Winter ecology of Spectacled Eiders: Environmental characteristics and population change. *Condor*, 106, 79-94.
PHILLIPS, V.E. (1991) Pochard *Aythya ferina* use of chironomid-rich feeding habitat in winter. *Bird Study*, 38, 118-122.
PIERSMA, T., & POOT, M.J.M. (1992) Where shorebirds may parallel penguins: spontaneous increase in locomotor activity triggered by fat depletion in a voluntarily fasting red knot. *Condor*.
PIERSMA, T., CAMPHUYSEN, K. (2001) What can peak mortalities of eiders tell us about the state of the Dutch Wadden Sea ecosystem? *Wadden Sea Newsletter 2001*, 1, 42 - 45.
POYSA, H. (1985) Circumstantial Evidence of Foraging Interference between 2 Species of Dabbling Ducks. *Wilson Bulletin*, 97, 541-543.
RAFFAELLI, D., FALCY, V. & GALBRAITH, C. (1990) Eider predation and the dynamics of mussel-bed communities. In Proceedings of the 24th European Marine Biological Symposium (ed M. Barnes, Gibson, R.N.), pp. 157 - 169. Aberdeen University Press.
REYNOLDS, P. (1987) Observation on the time budget and diving ecology of Long-tailed ducks in Eqalungmiut Nunaat, West Greenland. *Wildfowl*, 38, 55-62.
RICCIARDI, A., & BOURGET, E. (1998) Weight-to-weight conversion factors for marine benthic macro-invertebrates. *Marine Ecology Progress Series*, 163, 245 - 251.
RICHMAN, S.E. & LOVVORN, J.R. (2003) Effects of clam species dominance on nutrient and energy acquisition by spectacled eiders in the Bering Sea. *Marine Ecology Progress Series*, 261, 283-297.
RICHMAN, S.E. & LOVVORN, J.R. (2004) Relative foraging value to Lesser Scaup ducks of native and exotic clams from San Fransisco Bay. *Ecological Applications*, 14, 1217-1231.
RIZZOLO, D.J., and others (2005) Do wintering Harlequin Ducks forage nocturnally at high latitudes? *Condor*, 107, 173-177.
RODWAY, M.S. & COOKE, F. (2001) Effect of food availability on arrival and departure decisions of Harlequin Ducks at diurnal feeding grounds. *Condor*, 103, 870-874.
ROSS, B.P., LIEN, J., & FURNESS, R.W. (2001) Use of underwater playback to reduce the impact of elders on mussel farms. *Ices Journal of Marine Science*, 58, 517-524.
ROSS, B.P.F., R.W. (2000) *Minimising the impact of eider ducks on mussel farming.*, University of Glasgow, Glasgow.
ROSS, R.K. (1983) An estimate of the Black Scoter *Melanitta nigra,* population moulting in James and Hudson Bays. *Canadian Field Naturalist*, 97, 147-150.

SAVARD, J.P.L. & LAMOTHE, P. (1991) Distribution, abundance and aspects of breeding ecology of black scoters *Melanitta nigra* and surf scoters *M perspicillata* in Northern Quebec. *Canadian Field Naturalist*, 105, 488-496.
SCHEIFFARTH, G., KEMPF, N. & POTEL, P. (2001) Numbers and distribution of eider ducks *Somateria mollissima* in the German Wadden Sea in winter 1999/2000: Fleeing the fate of death? *Wadden Sea Newsletter 2001*, 1, 14 - 15.
SCHEIFFARTH, G. & NEHLS, G. (1997) Consumption of benthic fauna by carnivorous birds in the Wadden Sea. *Helgolander Meeresuntersuchungen*, 51, 373-387.
SCHENKEVELD, L.E. & YDENBERG, R. (1985) Synchronous diving by surf scoter flocks. *Canadian Journal of Zoology*, 63, 2516-2519.
SEKIYA, Y., HIRATSUKU, J., YAMAMURO, M., OKA, N. & ABE, M. (2000) Diet selectivity and shift of overwintering common pochards and tufted ducks in a eutrophic lagoon. *Journal of Marine Systems*, 26, 233 - 238.
SKERRATT, L.F., and others (2005) Causes of mortality in sea ducks (Mergini) necropsied at the USGS-National Wildlife Health Center. *Waterbirds*, 28, 193-207.
SMITH, L., HALL, C., WORDEN, J., HARRISON, A.L., ALLEN, L., BRADBURY, G., CRANSWICK, P.A., WOODWARD, R., SHEPHERD, P., PAYNTER, D. , MCGILL, M. (2006). Aerial surveys of waterbirds in The Wash, 2005/06, Rep. No. 708. English Nature Research Report.
STEMPNIEWICZ, L. (1986) The food intake of two scoters *Melanitta fusca* and *M.nigra* wintering in the Gulf of Gdansk, Polish Baltic coast. *Var Fagelvarld*, 11, 211-214.
STEPHENSON, R. (1994) Diving energetics in Lesser Scaup *Aythya affinis,* eyton. *Journal of Experimental Biology*, 190, 155-178.
STEPHENSON, R., BUTLER, P.J., & WOAKES, A.J. (1986) Duck diving behaviour. *Journal of Experimental Biology*, 126, 341-359.
STEPHENSON, R., and others (1989) A hydromechanical estimate of the power requirements of diving and surface swimming in Lesser Scaup *Aythya affinis*. *Journal of Experimental Biology*, 147, 507-519.
STEPHENSON, R., TURNER, D.L., & BUTLER, P.J. (1989) The Relationship between Diving Activity and Oxygen Storage Capacity in the Tufted Duck (Aythya-Fuligula). *Journal of Experimental Biology*, 141, 265-275.
STILLMAN, R.A., GOSS-CUSTARD, J.D., CLARKE, R.T., DURELL, S.E.A. LE.V.DIT. (1996) Shape of the interference function in a foraging vertebrate. *Journal of Animal Ecology*, 65, 813 - 824.
STILLMAN, R.A., CALDOW, R.W.G., GOSS-CUSTARD, J.D., ALEXANDER, M.J. (2000b) Individual variation in intake rate: the relative importance of foraging efficiency and dominance. *Journal of Animal Ecology*, 69, 484 - 493.
STILLMAN, R.A., GOSS-CUSTARD, J.D., WEST, A.D., DURELL, S.E.A. LE V. DIT., MCGRORTY, S., CALDOW, R.W.G., NORRIS, K. J., JOHNSTONE, I.G., ENS, B.J., VAN DER MEER, J. & TRIPLET, P. (2001) Predicting shorebird mortality and population size under different regimes of shellfishery management. *Journal of Applied Ecology*, 38, 857 - 868.
STILLMAN, R.A., WEST, A.D., GOSS-CUSTARD, J.D., CALDOW, R.W.G., MCGRORTY, S., DURELL, S.E.A. LE V. DIT., YATES, M.G., ATKINSON, P.W., CLARK, N.A., BELL, M.C., DARE, P.J. & MANDER, M. (2003) An individual behaviour-based model can predict shorebird mortality using

routinely collected shellfishery data. *Journal of Applied Ecology*, 40, 1090 - 1101.
STILLMAN, R.A., CLARK, N.A., ATKINSON, P.W., WEST, A.D., MCGRORTY, S., DURELL, S.E.A. LE V. DIT. & YATES, M.G. (2004). Assessing the impacts of shell-fishing and mussel farming on Oystercatcher populations in the Wash, England. Phase 1: Identification of model parameters to be refined.
STILLMAN, R.A., WEST, A.D., GOSS-CUSTARD, J.D., MCGRORTY, S., FROST, N.J., MORRISEY, D.J., KENNY, A.J. & DREWITT, A.L. (2005a) Predicting site quality for shorebird communities: a case study on the Humber estuary, UK. *Marine Ecology Progress Series*, 305, 203 - 217.
STILLMAN, R.A., CALDOW, R.W.G., DURELL, S.E.A.LE. V. DIT., WEST, A.D., MCGRORTY, S., GOSS-CUSTARD, J.D., PEREZ-HURTADA, A., CASTRO, M., ESTRELLA, S., MASERO, A.J., RODRIGUEZ-PASCAL, F.H., TRIPLET, P., LOQUET, N., DESPREZ, M., FRITZ, H., CLAUSEN, P., EBBINGE,E., NORRIS, K. & MATTISON, E. (2005b). Maintaining migratory coastal bird diversity: management through individual-based predictive population modelling. Centre for Ecology and Hydrology.
STILLMAN, R.A., and others (2000a) Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. *Journal of Applied Ecology*, 37, 564-588.
STOTT, R.S. & OLSON, D.P. (1973) Food-habitat relationship of sea ducks on the New Hampshire coastline. *Ecology*, 54, 996-1007.
SUTER, W. & VAN EERDEN, M.R. (1992) Simultaneous Mass Starvation of Wintering Diving Ducks in Switzerland and the Netherlands - a Wrong Decision in the Right Strategy. *Ardea*, 80, 229-242.
SWENNEN, C. (1976) Population-Structure and Food of Eider Somateria M Mollissima in Dutch Wadden Sea. *Ardea*, 64, 311-371.
SWENNEN, C., NEHLS, G. & LAURSEN, K. (1989) Numbers and distribution of eiders *Somateria mollissima* in the Wadden Sea. *Netherlands Journal of Sea Research*, 24, 83 - 92.
SWENNEN, C., LEOPOLD, M.F. & DE BRUIJN, L.L.M. (1989) Time-stressed oystercatchers, *Haematopus ostralegus*, can increase their intake rate. . *Animal Behaviour*, 38, 8 - 22.
SWENNEN, C., DUIVEN, P., & REYRINK, L.A. (1979) Notes on the Sex-Ratio in the Common Eider Somateria-Mollissima (L). *Ardea*, 67, 54-61.
SWENNEN, C., NEHLS, G., & LAURSEN, K. (1989) Numbers and Distribution of Eiders Somateria-Mollissima in the Wadden Sea. *Netherlands Journal of Sea Research*, 24, 83-92.
SYSTAD, G.H. & BUSTNES, J.O. (2001) Coping with darkness and low temperatures: foraging stategies in Steller's eiders, *Polysticta stelleri*, wintering at high latitudes. *Canadian Journal of Zoology*, 79, 402-406.
SYSTAD, G.H., BUSTNES, J.O., & ERIKSTAD, K.E. (2000) Behavioural responses to decreasing day length in wintering sea ducks. *The Auk*, 117, 33-40.
TOME, M.W. (1988) Optimal foraging: food patch depletion by ruddy ducks. *Oecologia*, 76, 27-36.
TOME, M.W. (1989) Food patch depletion by ruddy ducks: foraging by expectation rules. *Canadian Journal of Zoology*, 67, 2751-2755.
TOME, M.W. (1989) Search-path characteristics of foraging ruddy ducks. *The Auk*, 106, 42-48.

TOME, M.W. & WRUBLESKI, D.A. (1988) Underwater foraging behaviour of canvasbacks, lesser scaups and ruddy ducks. *The Condor*, 90, 168-172.
TRIPLET, P., STILLMAN, R.A., GOSS-CUSTARD, J.D. (1999) Prey abundance and the strength of interference in a foraging shorebird. *Journal of Animal Ecology*, 68, 254 - 265.
VAN DEN BERK, V.M., DIRKSEN, S., POOT, M.J.M. (2001) Mortality of eiders in the Dutch Wadden Sea 1999/2000: The search for the cause of mass mortality of eiders in the Dutch Wadden Sea. *Wadden Sea Newsletter 2001*, 1, 46 - 47.
VAN GILS, J.A., DEKINGA, A., SPAANS, B., VAHL, W.K. & PIERSMA, T. (2005a) Digestive botleneck affects foraging decisions in red knot *calidris canutus*. II. Patch choice and length of working day. *Journal of Animal Ecology*, 74, 120 - 130.
VAN GILS, J.A., and others (2005b) Digestive bottleneck affects foraging decisions in red knots Calidris canutus. I. Prey choice. *Journal of Animal Ecology*, 74, 105-119.
WALTON, P., RUXTON, G.D., & MONAGHAN, P. (1998) Avian diving, respiratory physiology and the marginal value theorem. *Animal Behaviour*, 56, 165-174.
WEST, A.D., GOSS-CUSTARD, J.D., STILLMAN, R.A., CALDOW, R.W.G., DURELL, S.E.A. LE V. DIT. & MCGRORTY, S. (2002) Predicting the impacts of disturbance on shorebird mortality using a behaviour-based model. *Biological Conservation*, 106, 319 - 328.
WEST, A.D., GOSS-CUSTARD, J.D., MCGRORTY, S., STILLMAN, R.A., & 5 OTHERS (2003) The Burry shellfishery and oystercatchers: using a behaviour-based model to advise shellfishery management policy. *Marine Ecology Progress Series*, 248, 279-292.
WILSON, R.P., and others (1992) Diving birds in cold water: do Archimedes and Boyle determine energetic costs? *The American Naturalist*, 140, 179-200.
WILSON, R.P. & QUINTANA, F. (2004) Surface pauses in relation to dive duration in imperial cormorants; how much time for a breather? *Journal of Experimental Biology*, 207, 1789-1796.
WINFIELD, I.J. & WINFIELD, D.K. (1994) Feeding Ecology of the Diving Ducks Pochard (Aythya-Ferina), Tufted Duck (a-Fuligula), Scaup (a-Marila) and Goldeneye (Bucephala-Clangula) Overwintering on Lough-Neagh, Northern-Ireland. *Freshwater Biology*, 32, 467-477.
WOAKES, A.J. & BUTLER, P.J. (1983) Swimming and diving in tufted ducks *Aythya fuligula* with particular reference to heart rate and gas exchange. *Journal of Experimental Biology*, 107, 311-329.
YATES, M., STILLMAN, R.A., GOS-CUSTARD, J.D. (2000) Contrasting interference functions and foraging dispersion in two species of shorebird (Charadrii). *Journal of Animal Ecology*, 69, 314 - 322.
YATES, M., GARBUTT, A., RISPIN, E., BROWN, N. (2004). Low tide survey of The Wash Special Protection Area. Final report of the winter 2002-2003 shorebird survey., Rep. No. 589. English Nature Research Report.
YDENBERG, R. & GUILLEMETTE, M. (1991) Diving and Foraging in the Common Eider. *Ornis Scandinavica*, 22, 349-352.
ZWARTS, L., ENS, B.J., GOSS-CUSTARD, J.D., HULSCHER, J.B. & DURELL, S.E.A.LE.V.DIT. (1996a) Causes of variation in prey profitability and its consequences for the intake rate of the oystercatcher *Haematopus ostralegus*. *Ardea*, 84A, 229 - 268.

ZWARTS, L., ENS, B.J., GOSS-CUSTARD, J.D., HULSCHER, J.B. & KERSTEN, M. (1996b) Why oystercatchers *Haematopus ostralegus* cannot meet their daily energy requirements in a single low water period. *Ardea*, 84A, 269 - 290.

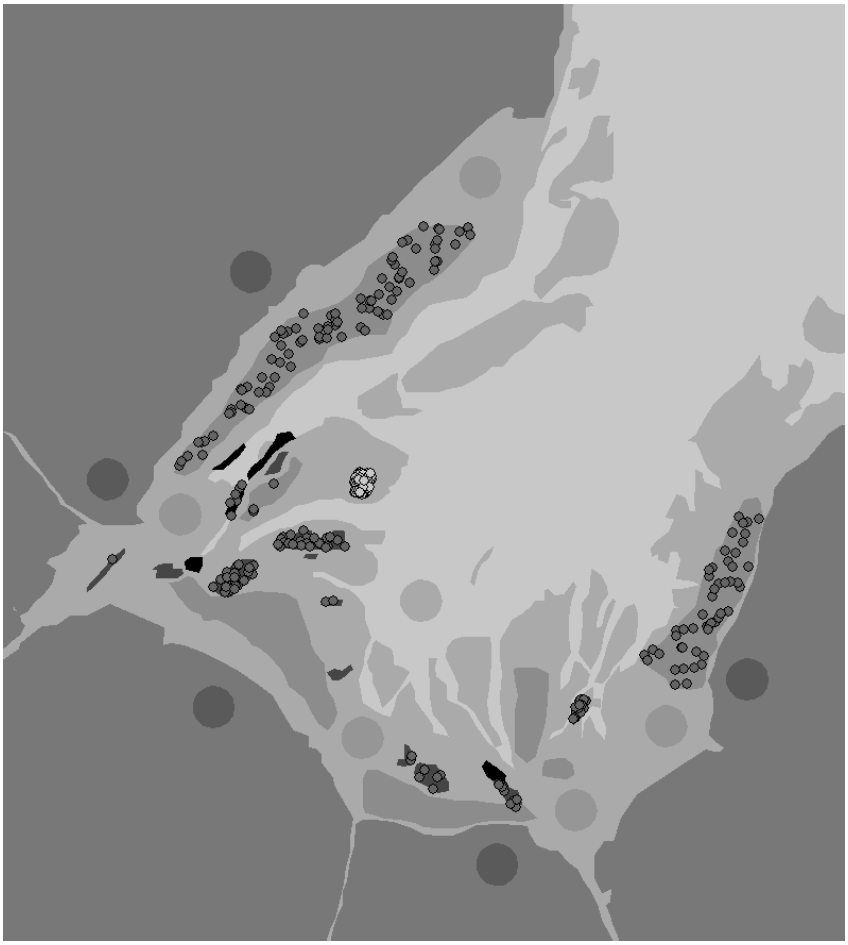

Figure 3.1 Screenshot of the model of the Wash. The dark grey areas around the margins of the image depict the land surrounding The Wash. The palest grey areas in the centre of the image are subtidal. The mid-grey areas between the subtidal areas and the areas of land depict the boundaries of the intertidal sand and mud flats. The birds in the model cannot utilise any of these patches which were included in the model simply to create a background against which to visualise the distribution of birds between the available patches. With the exception of the patch of *Ensis*, which is subtidal (and depicted by the grey circle in the sub-tidal area), all of the other resource patches are intertidal and are shown as darker grey areas within the boundaries of the intertidal sand and mud flats in positions that approximate their position in reality (bearing in mind that some of the model patches represent amalgamations of spatially discrete patches in reality). Mussel lays are shown as black (when exposed by the tide).Regulated mussel beds exposed by the tide are shown as the darkest shade of grey and exposed cockle beds as the next darkest shade of grey. The five pale grey circles within the intertidal sand and mud flats depict the five patches on which oystercatchers are allowed to feed on the supplementary resources available on upshore flats on the advancing and receding tide. The five dark grey circles on the land denote the notional locations of the sites used by oystercatchers to roost around The Wash. Each of the small white circles represents an eider duck and each small dark circles represents an oystercatcher.

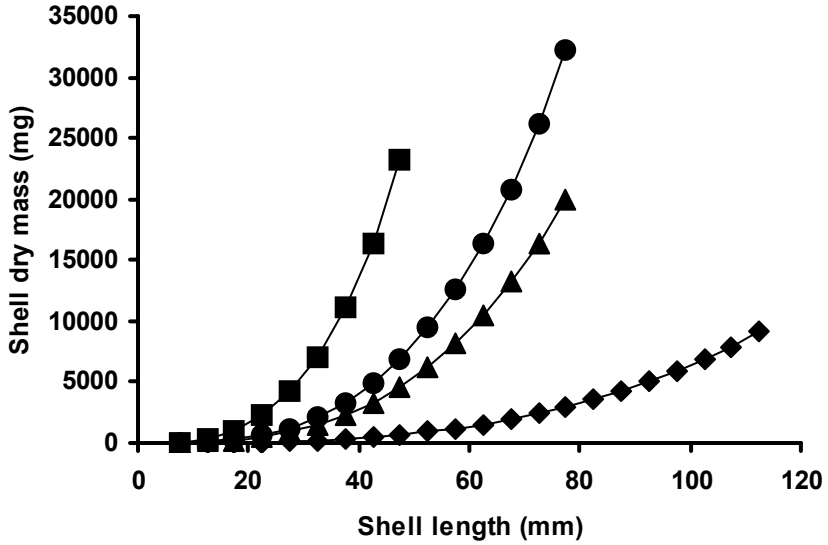

Figure 3.2 Relationships between shell dry mass (mg) and shell length (mm) used in the model for cockles (squares), natural mussels (circles), lay mussels (triangles) and *Ensis* (diamonds). See Table 3.2 for equations and sources of information.

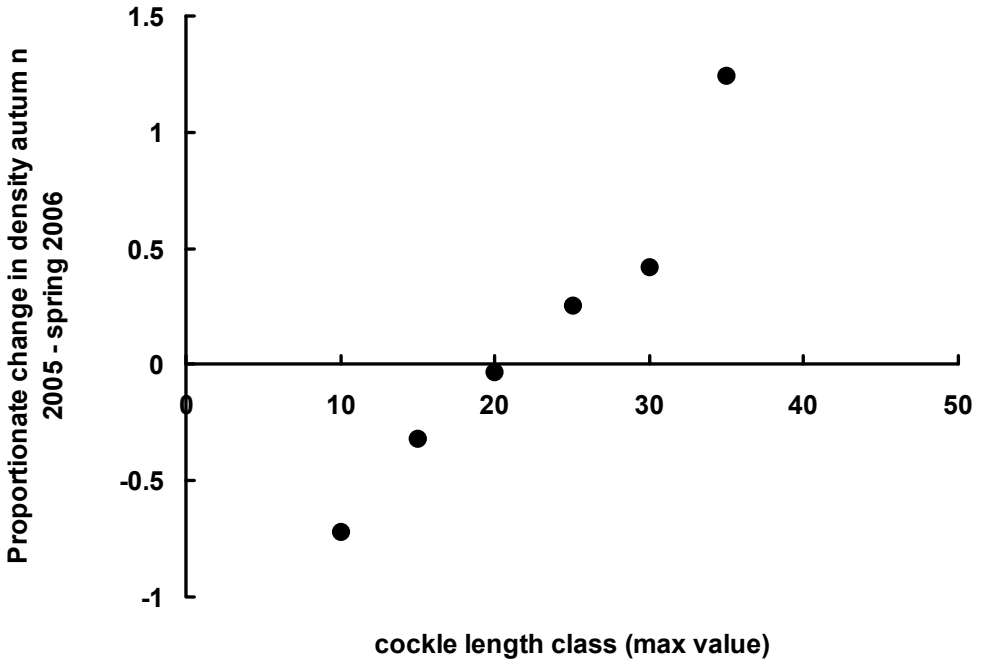

Figure 3.3 Relationship between the average over-winter proportionate change in the numerical density of cockles and their size derived from analysis of the results of the surveys of several cockle beds in autumn 2005 and spring 2006 by ESFJC.

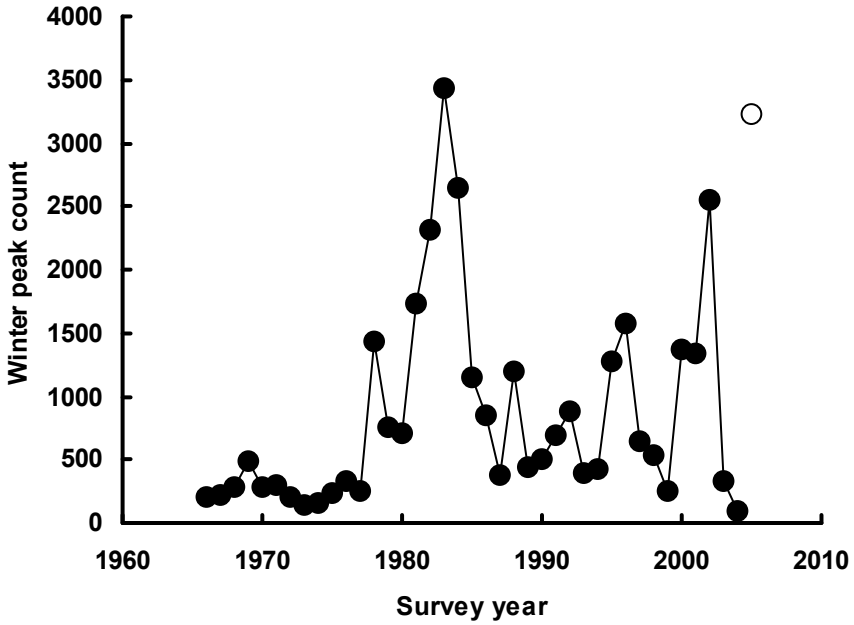

Figure 3.4 Winter maxima counts for eider ducks in The Wash. Values derived from WeBS counts with the exception of the open symbol which denotes the peak count of 3224 eider counted on 6th February 2006 by Hart & Brown (2006).

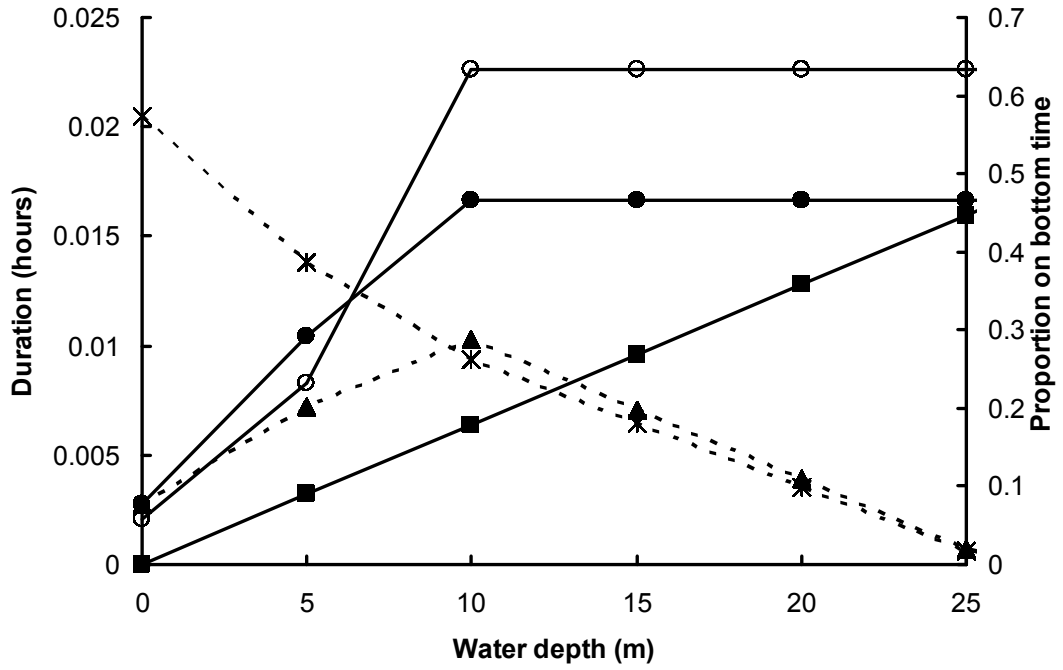

Figure 3.5 The diving sub model within the model MORPH is based on the relationships between the depth of water and: i) the total time spent underwater per dive (filled circles), ii) the time spent on the water surface between dives (open circles), iii) the time spent in transit between the surface and the seabed per dive (filled squares), iv) the time spent on the seabed per dive (filled triangles) and v) the resultant proportion of a dive cycle that is spent feeding on the bottom (asterisks). In the model of The Wash, the maximum water depth over any of the shellfish patches is 8.12m.

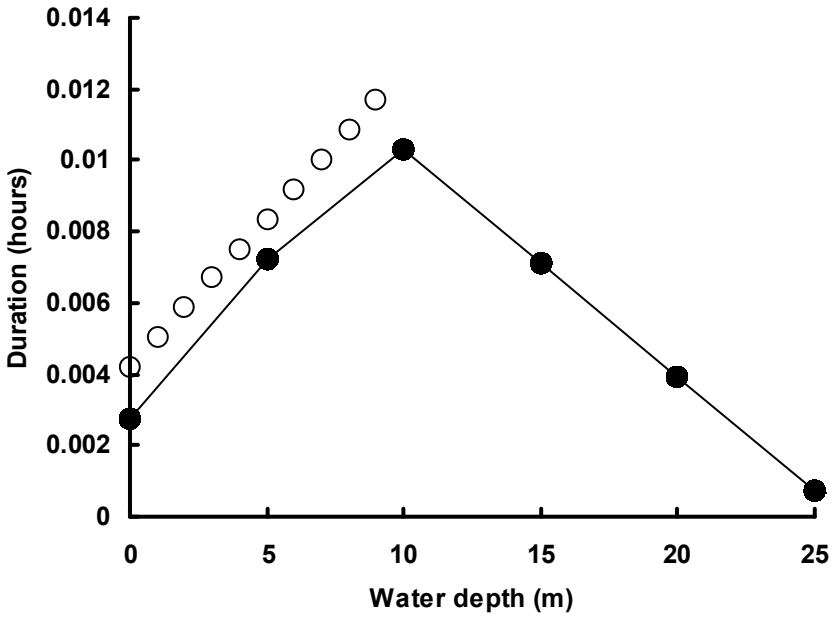

Figure 3.6 Relationship between the amount of time spent on-bottom per dive and water depth as represented in the model MORPH (closed symbols) and as derived by subtraction of predicted travel time from predicted dive time of two female eiders studied in winter by Guillemette and others (2004) (open symbols).

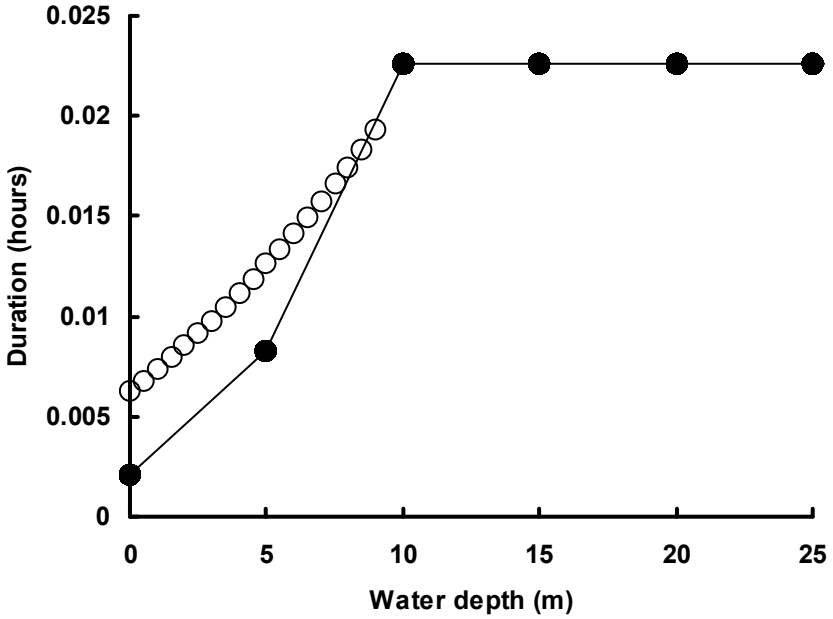

Figure 3.7 Relationship between the amount of time spent on the surface between successive dives as represented in the model MORPH (closed symbols) and as derived from the relationships between dive duration and water depth presented by Guillemette and others (2004) and the relationship between surface duration and dive duration presented by Ydenberg & Guillemette (1991) (open symbols).

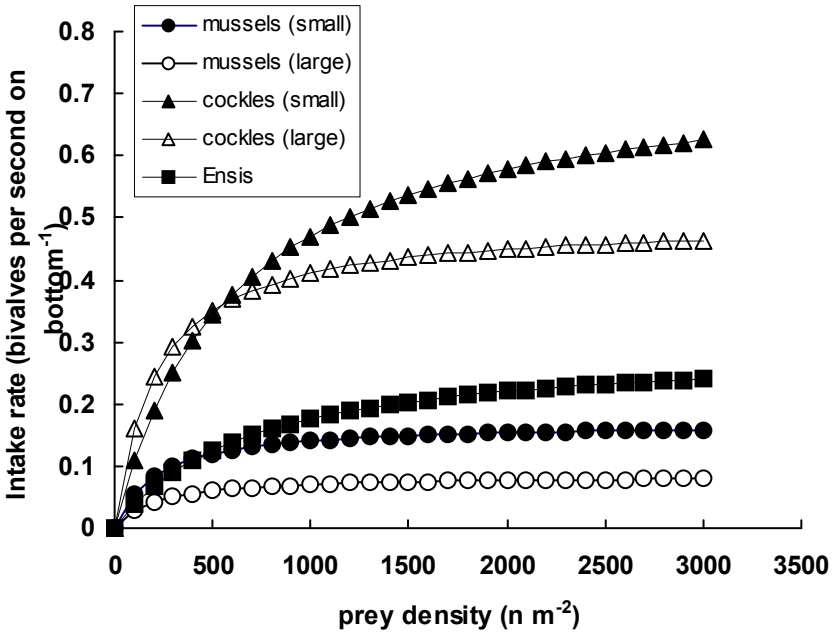

Figure 3.8 Relationship between the rate at which eiders consume various diets in the model and the density of bivalves belonging to those diets. Derived from data provided by Nehls (1995) and Richman & Lovvorn (2003) (see section 3.7.4).

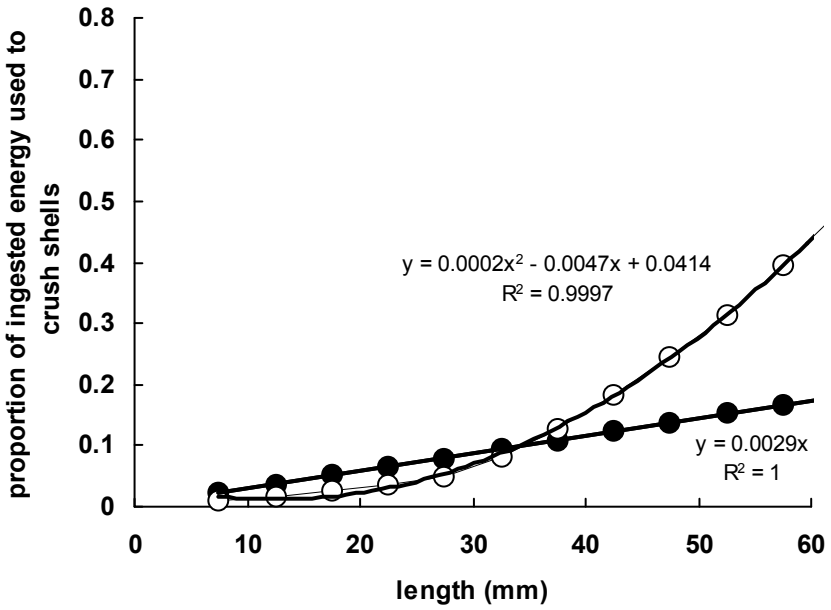

Figure 3.9 Relationship between mussel length and the proportion of ingested energy content that is expended in crushing the shell for lay mussels (closed symbols) and mussels from regulated beds (open symbols). Note that eiders only consume mussels up to 50mm length in the model.

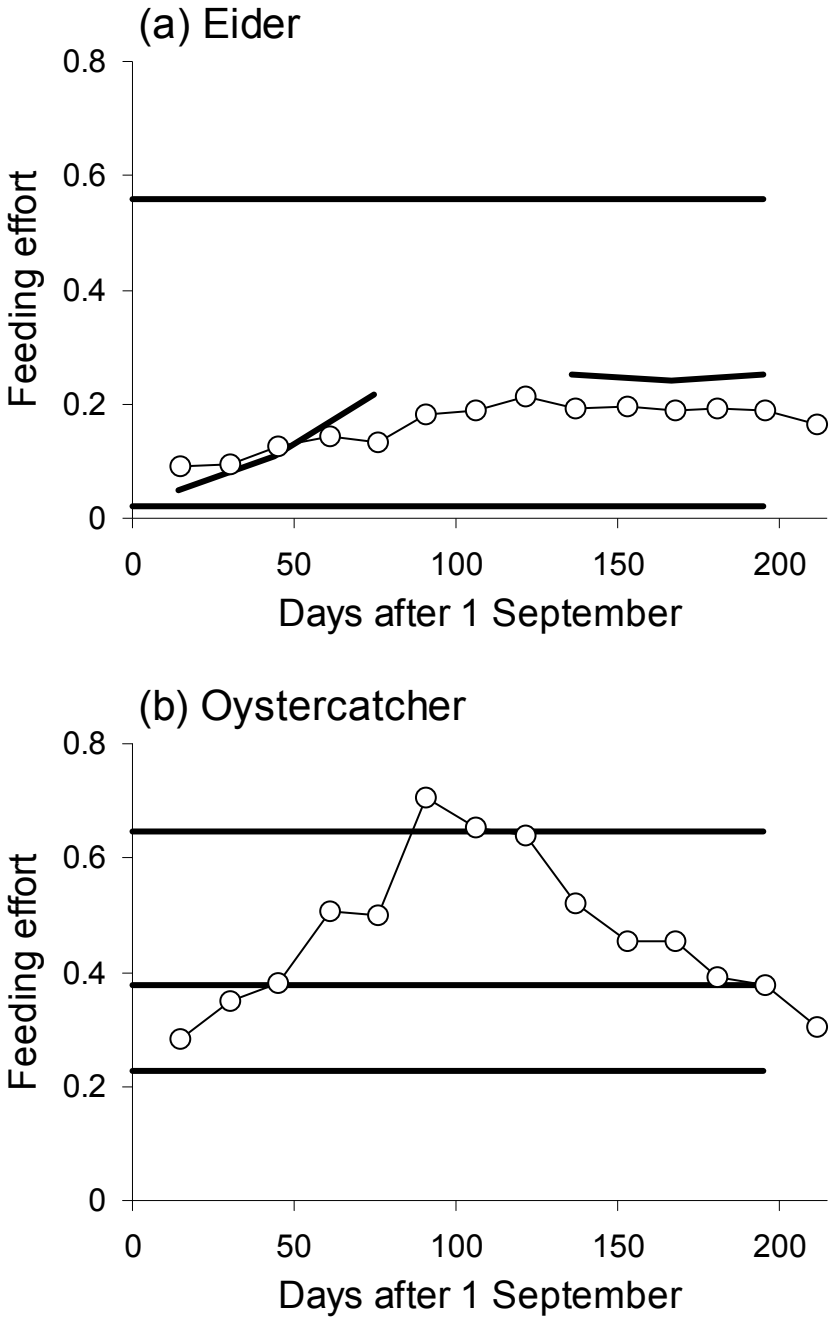

Figure 5.1 Seasonal variation in the predicted proportion of time spent actively feeding by a) eiders and b) oystercatchers in comparison with empirical data. Each point represents the mean (across five replicate simulations) predicted proportion of daylight hours spent feeding on the middle and last day of each month between September and March. The upper and lower solid lines depict maximum and minimum values derived from the literature (see text). In a) the broken solid line depicts the data of Nehls (1995). In b) the middle solid line depicts the mean value derived from the literature.

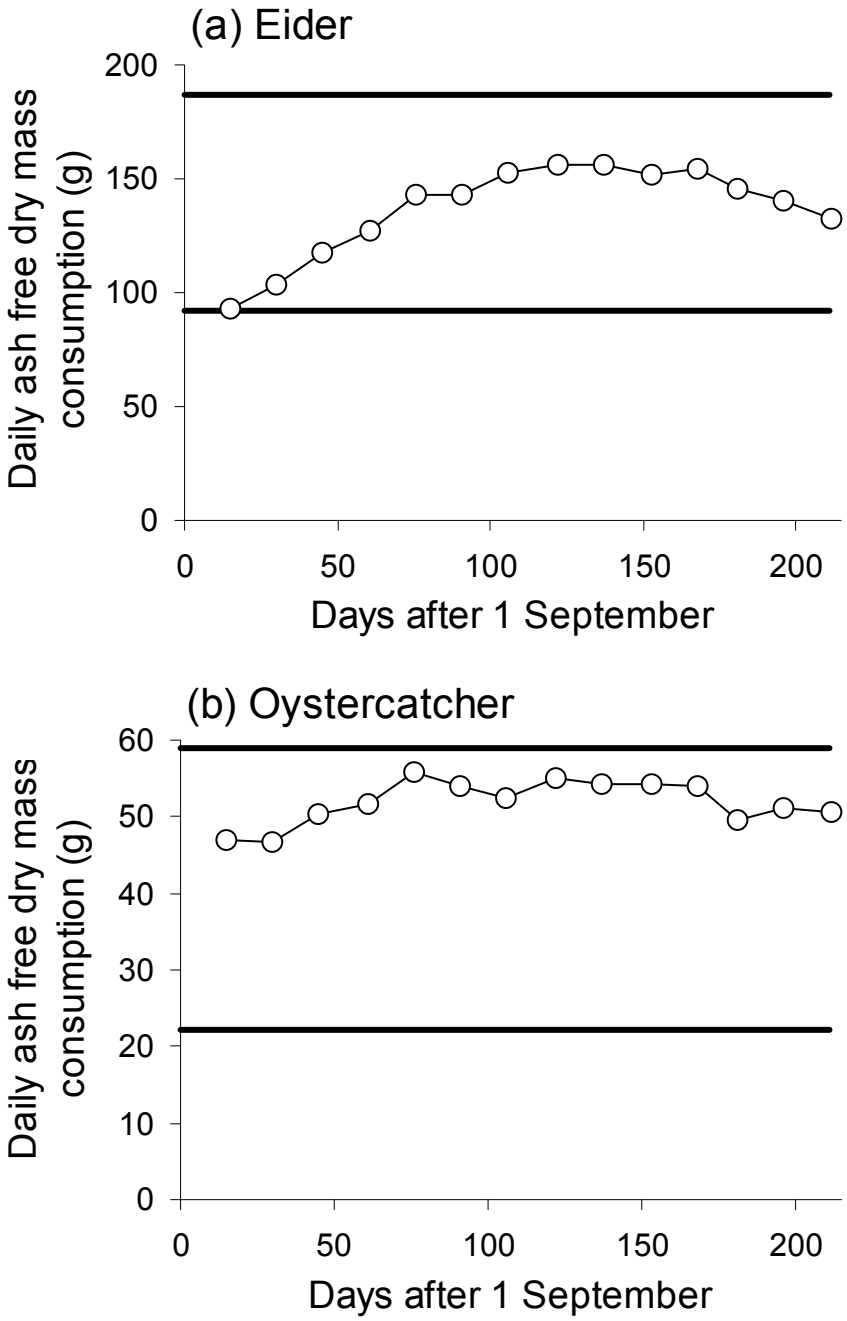

Figure 5.2 Seasonal variation in the predicted daily consumption of ash-free dry mass of bivalve prey by a) eiders and b) oystercatchers in comparison with likely upper and lower limits derived from independent empirical data. Each point represents the mean (across five replicate simulations) predicted daily food consumption on the middle or last day of each month between September and March. The upper and lower horizontal bars depict the likely bounds throughout most of the modelled period, based on the literature review.

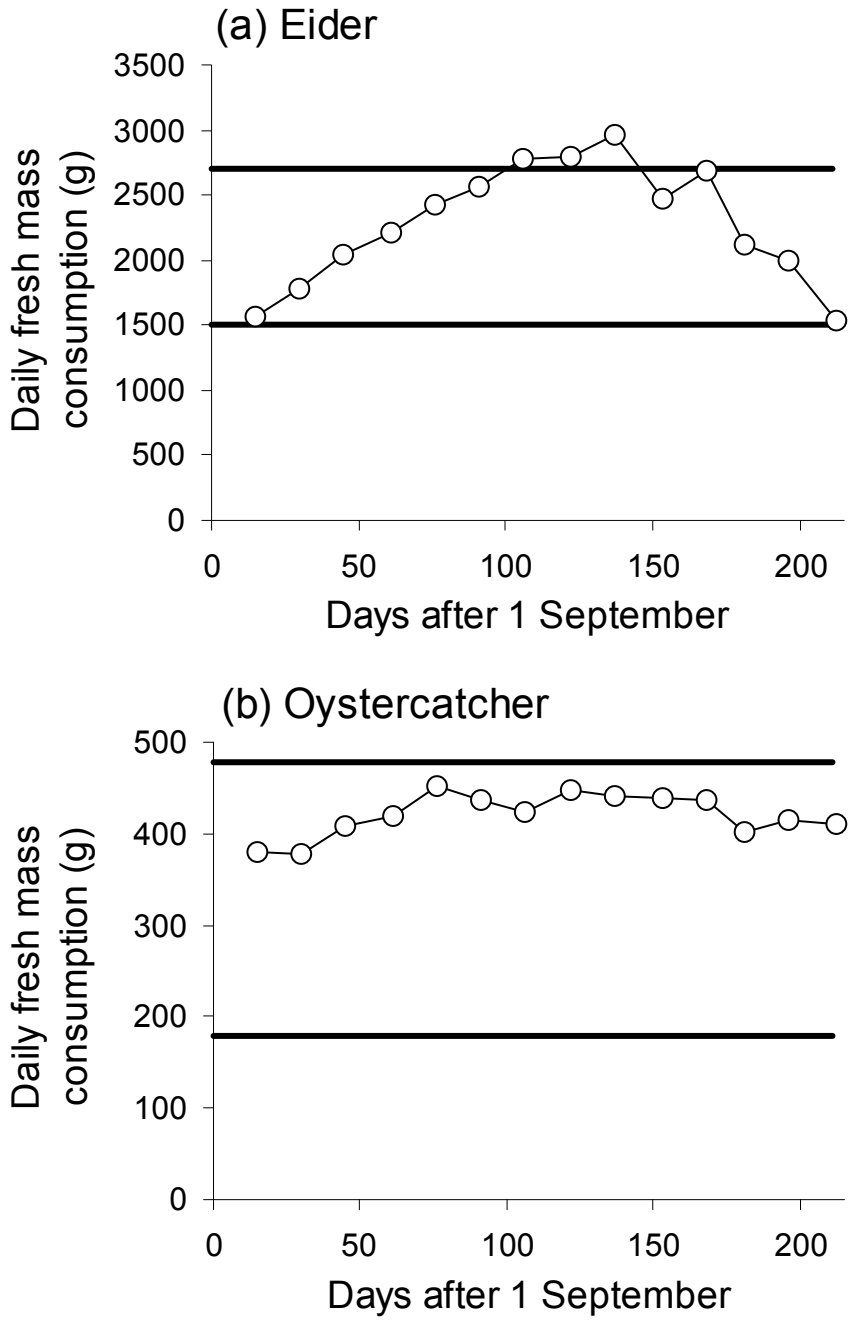

Figure 5.3 Seasonal variation in the predicted daily consumption of fresh mass of bivalve prey by a) eiders (shell mass included) and b) oystercatchers (wet flesh only) in comparison with likely upper and lower limits derived from independent empirical data. Each point represents the mean (across five replicate simulations) predicted daily food consumption on the middle or last day of each month between September and March. The upper and lower horizontal bars depict the likely bounds throughout most of the modelled period, based on the literature review.

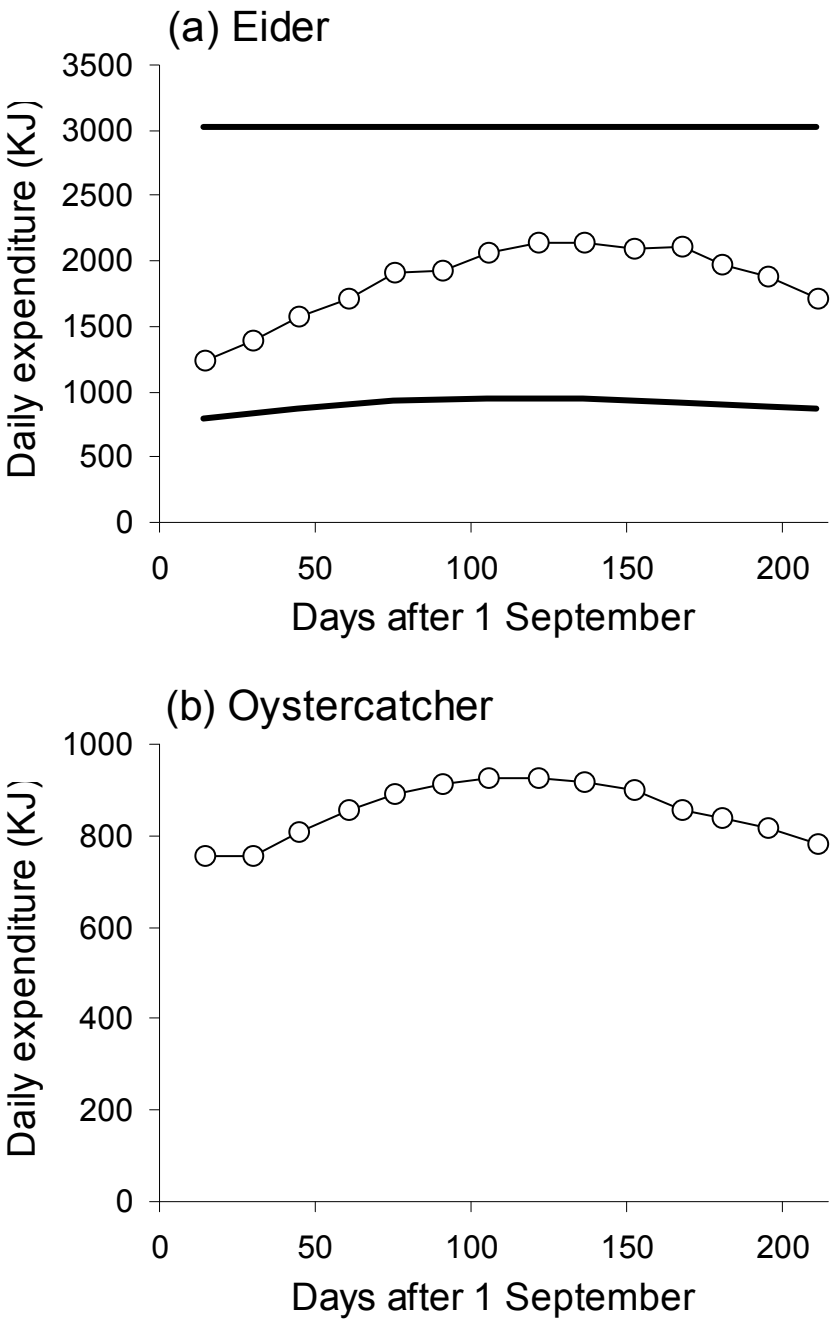

Figure 5.4 Seasonal variation in the predicted daily energy expenditure of a) eiders and b) oystercatchers. Each point represents the mean (across five replicate simulations) predicted daily energy expenditure on the middle and last day of each month between September and March. In a) the upper horizontal line depicts a value of 3,022kJ equivalent to 4.3 * BMR, assumed to be the likely upper bound to eiders' DEE, whereas the lower solid line represents the predicted seasonal variation in eiders' temperature-dependent resting metabolic rate.

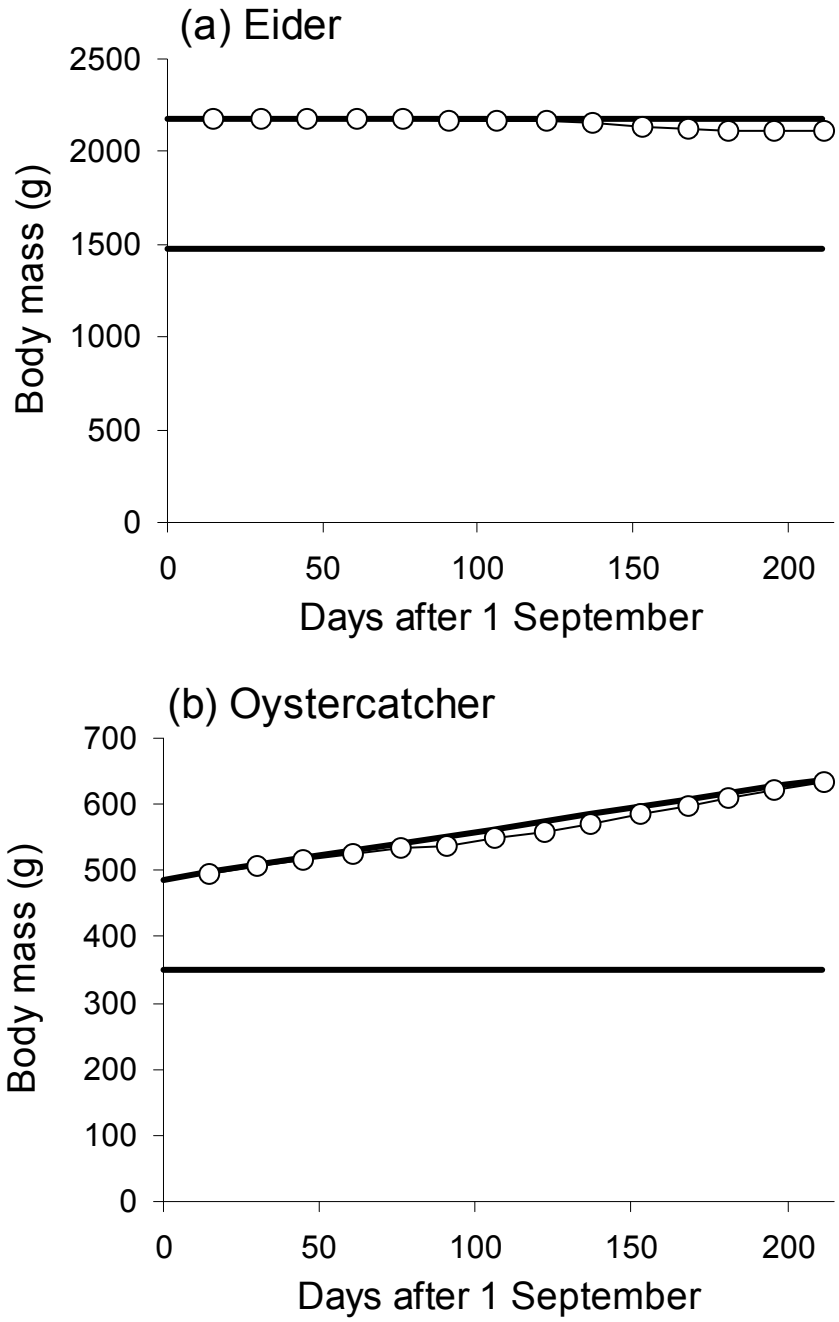

Figure 5.5 Seasonal variation in the predicted mean body mass (open circles) of a) eiders and b) oystercatchers in comparison with their assumed target body mass (upper thick solid line) and starvation mass (lower thick solid line). Each point represents the mean (across five replicate simulations) predicted body mass on the middle and last day of each month between September and March of those birds present in the model and alive on the day in question.

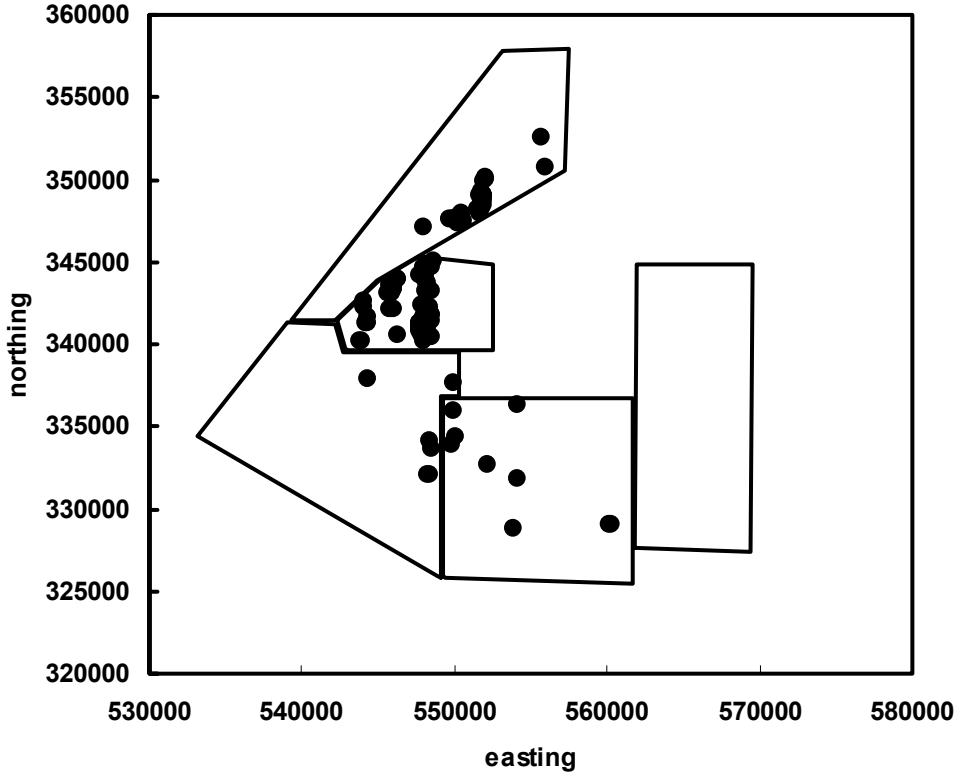

Figure 5.6 The location of each sighting of eider ducks made on 5 over flights between November 2005 and March 2006 (Smith, Hall, Worden, Harrison, Allen, Bradbury, Cranswick, Woodward, Shepherd, Paynter & McGill 2006), superimposed upon the boundaries of the five principal regions of The Wash defined in order to facilitate a broad-scale comparison of the observed and predicted distribution of birds.

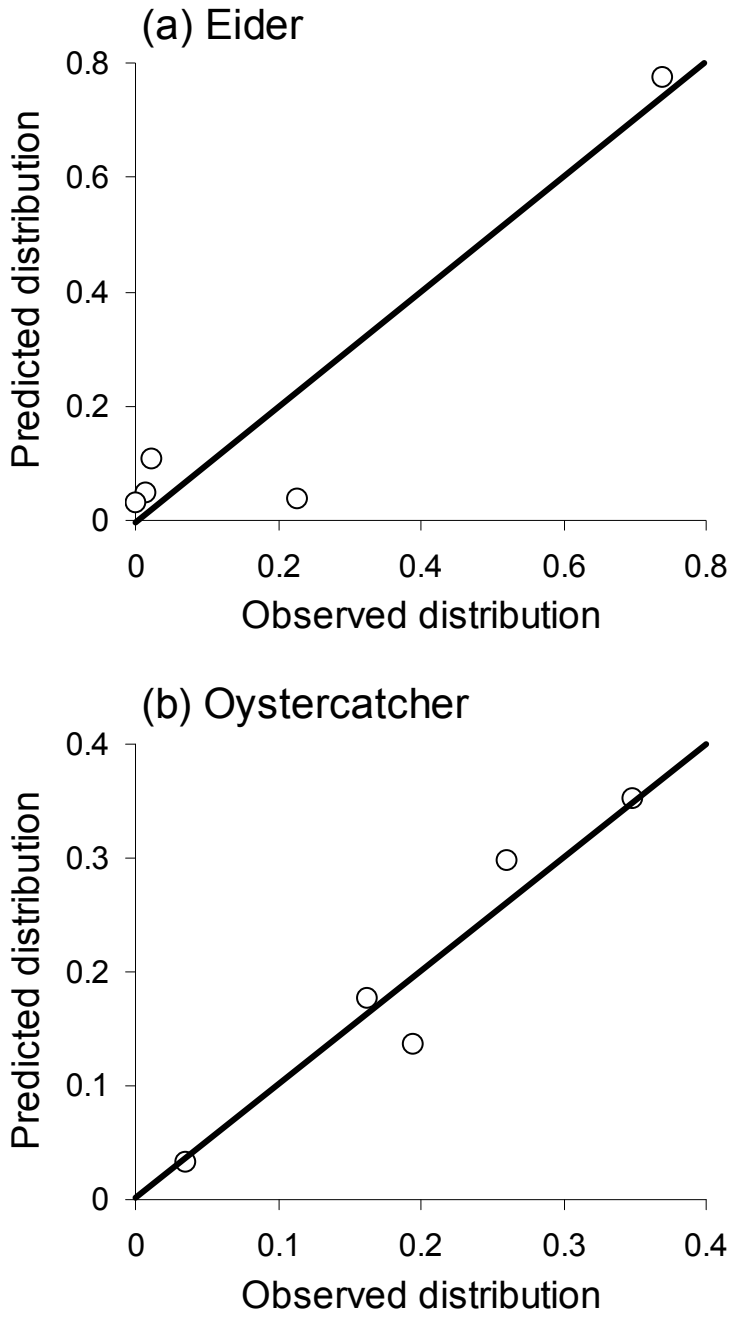

Figure 5.7 Relationship between the average overwinter proportion of the population of a) eiders and b) oystercatchers predicted by the model to occur within each of 5 regions of The Wash in comparison with the actual average overwinter proportion as recorded during the over flight surveys between November 2005 and March 2006. Each point represents the mean predicted value across five replicate simulations.

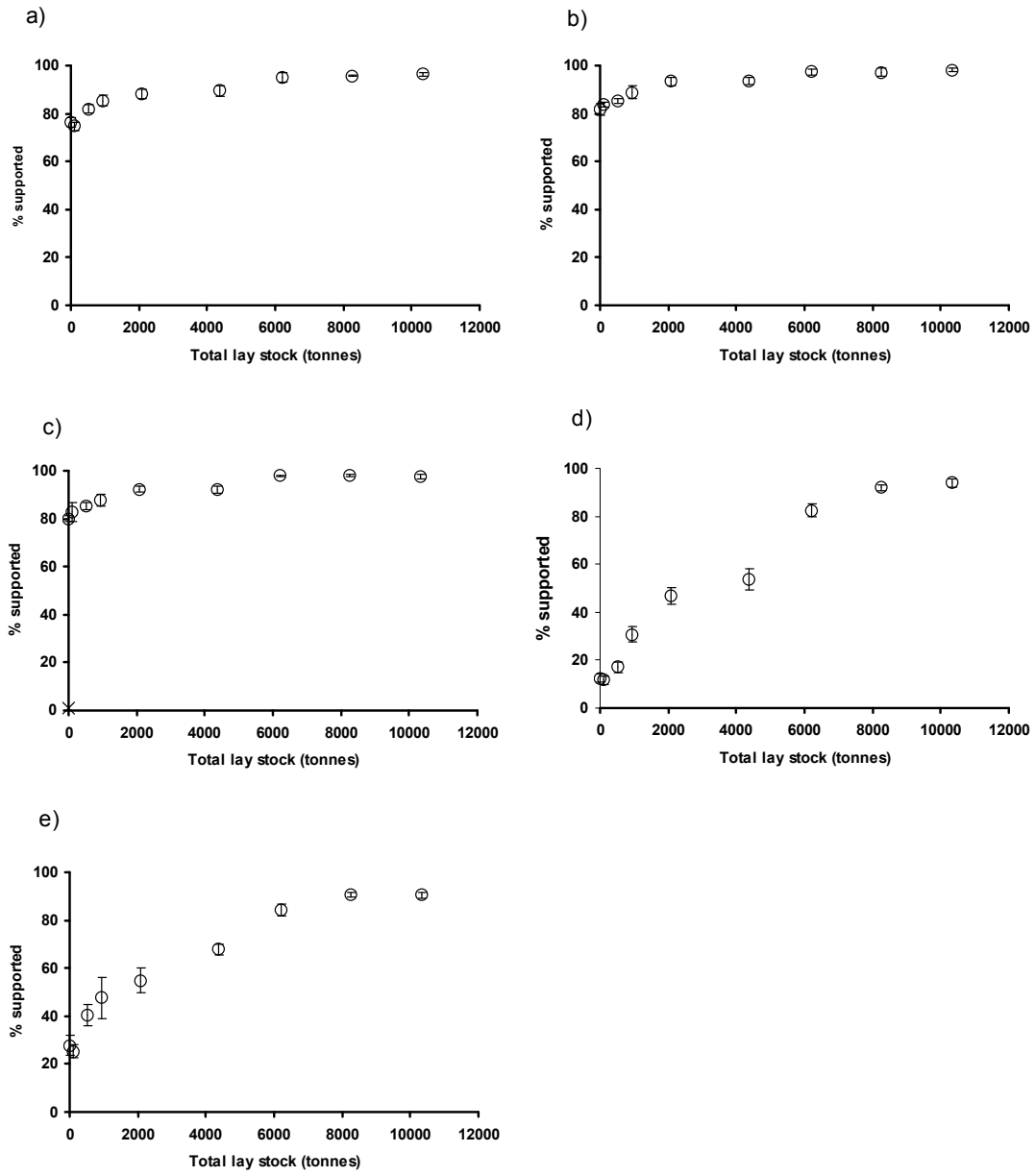

Figure 6.1 The effect of variation in the scale of the commercially cultivated lay mussel industry on the percentage of the eider population supported by the shellfish resources in The Wash against five alternative background shellfish resource levels. a) Scenario 1 -cockles and regulated mussels: medium, *Ensis* high b) Scenario 2 - cockles low, regulated mussels low, *Ensis* high c) Scenario 3 - cockles very low, regulated mussels low, *Ensis* high d) Scenario 4 - cockles and regulated mussels: medium, *Ensis* low e) Scenario 5 - cockles and regulated mussels high, *Ensis* low (see Table 4.2 for details of the values used). Each point represents the mean (+/- 2se) percentage of the population supported, averaged across three replicate simulations.

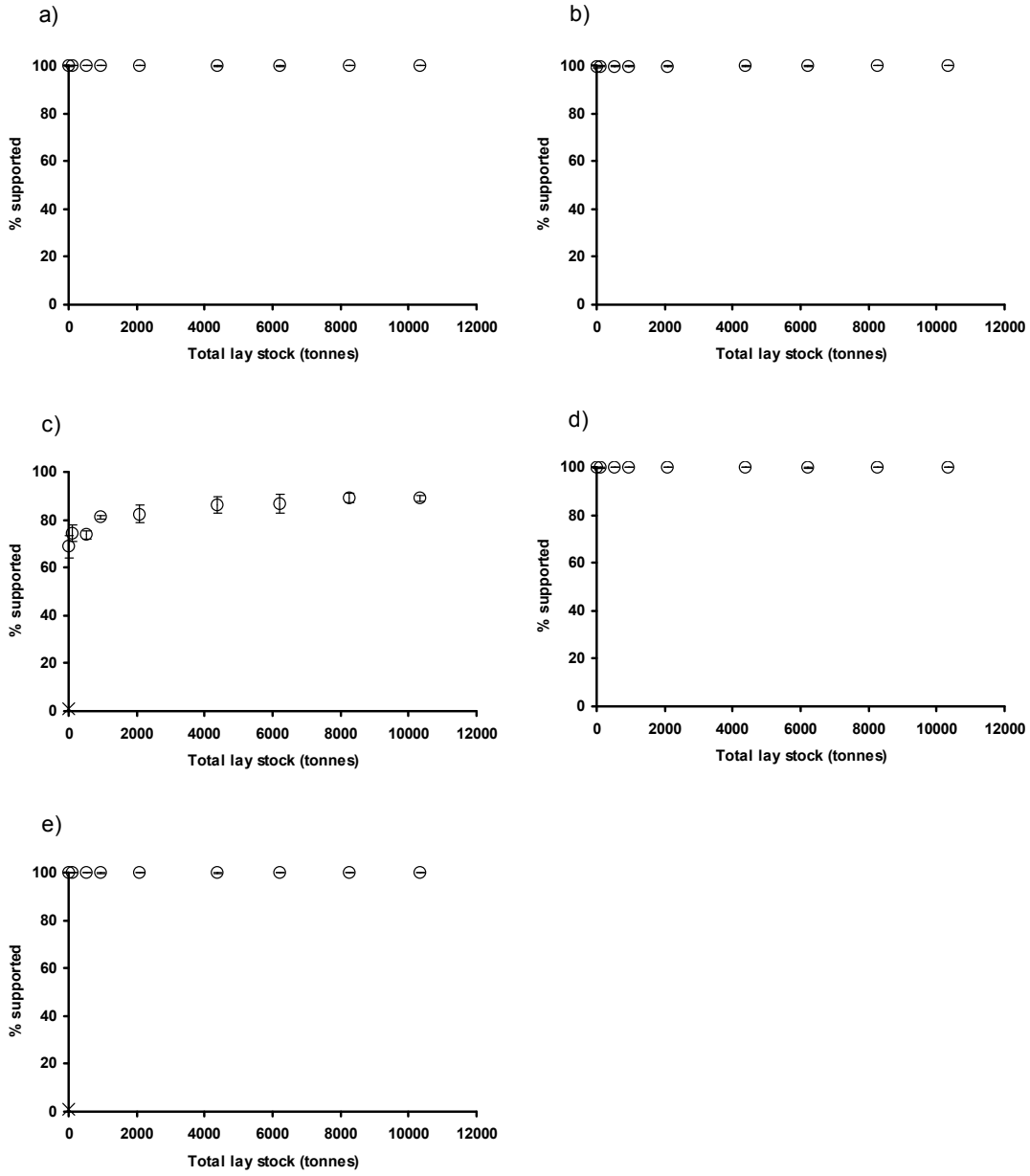

Figure 6.2 The effect of variation in the scale of the commercially cultivated lay mussel industry on the percentage of the oystercatcher population supported by the shellfish resources in The Wash against five alternative background shellfish resource levels. a) Scenario 1 -cockles and regulated mussels: medium, *Ensis* high b) Scenario 2 - cockles low, regulated mussels low, *Ensis* high c) Scenario 3 - cockles very low, regulated mussels low, *Ensis* high d) Scenario 4 - cockles and regulated mussels: medium, *Ensis* low e) Scenario 5 - cockles and regulated mussels high, *Ensis* low (see Table 4.2 for details of the values used). Each point represents the mean (+/-2se) percentage of the population supported, averaged across three replicate simulations.

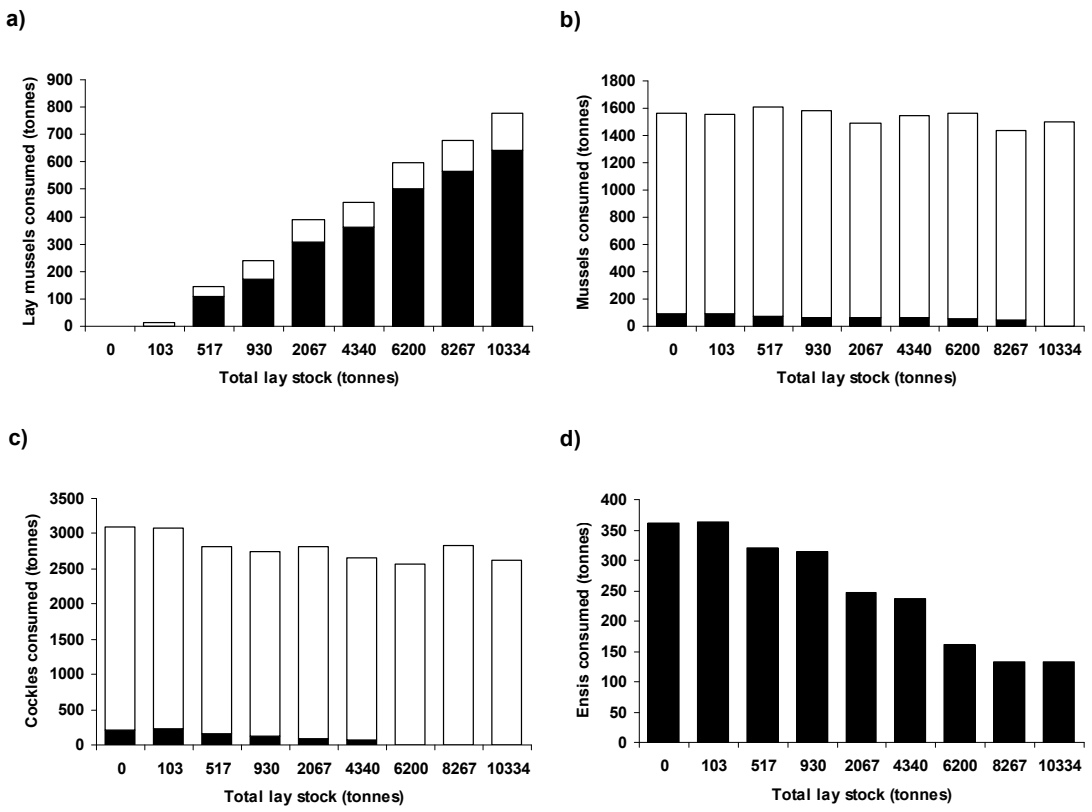

Figure 6.3 Total tonnage of shellfish removed overwinter from each of the four principal resource stocks by eiders (solid bars) and oystercatchers (open bars) as the total tonnage of lay mussels is reduced from the present day value of c 10,000t in a series of steps by gradually reducing the area and then removing lays in sequence as described in Table 4.1. a) Lay mussels, b) Regulated mussels, c) Cockles, d) *Ensis*. Background resource levels of cockles and regulated mussels are assumed to be medium and *Ensis* to be high ie Scenario 1 (see Table 4.2 for details of the values used). Note the different scales of the y axes shown in these figures.

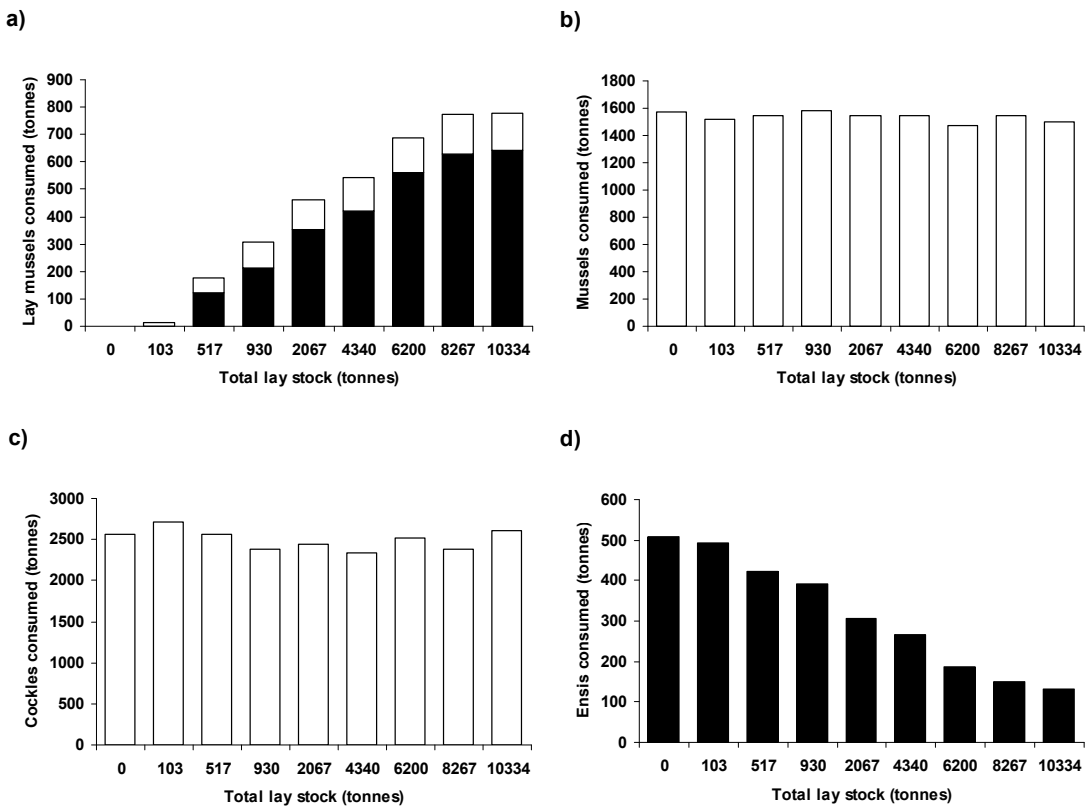

Figure 6.4 Total tonnage of shellfish removed overwinter from each of the four principal resource stocks by eiders (solid bars) and oystercatchers (open bars) as the total tonnage of lay mussels is reduced from the present day value of c 10,000t in a series of steps by gradually reducing the area and then removing lays in sequence as described in Table 4.1. a) Lay mussels, b) Regulated mussels, c) Cockles, d) *Ensis*. Background resource levels of cockles and regulated mussels are assumed to be low and *Ensis* to be high ie Scenario 2 (see Table 4.2 for details of the values used). Note the different scales of the y axes shown in these figures.

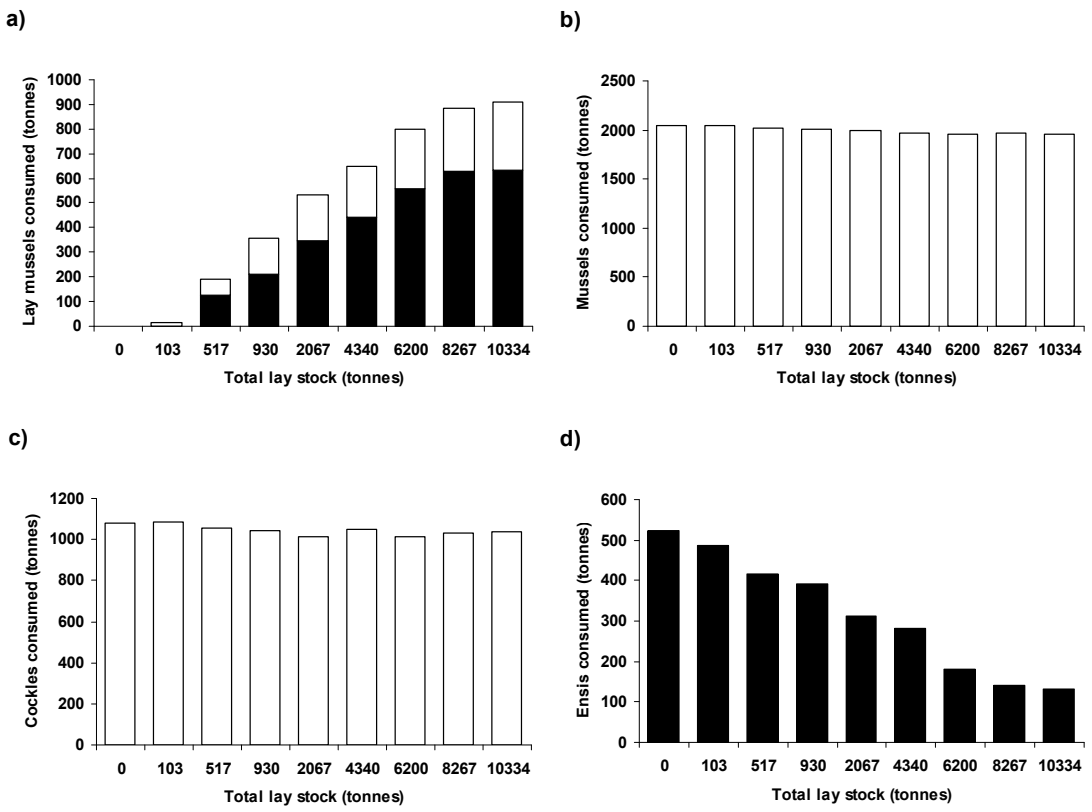

Figure 6.5 Total tonnage of shellfish removed overwinter from each of the four principal resource stocks by eiders (solid bars) and oystercatchers (open bars) as the total tonnage of lay mussels is reduced from the present day value of c 10,000t in a series of steps by gradually reducing the area and then removing lays in sequence as described in Table 4.1. a) Lay mussels, b) Regulated mussels, c) Cockles, d) *Ensis*. Background resource levels of cockles and regulated mussels are assumed to be very low and low respectively while *Ensis* is assumed to be high ie Scenario 3 (see Table 4.2 for details of the values used). Note the different scales of the y axes shown in these figures.

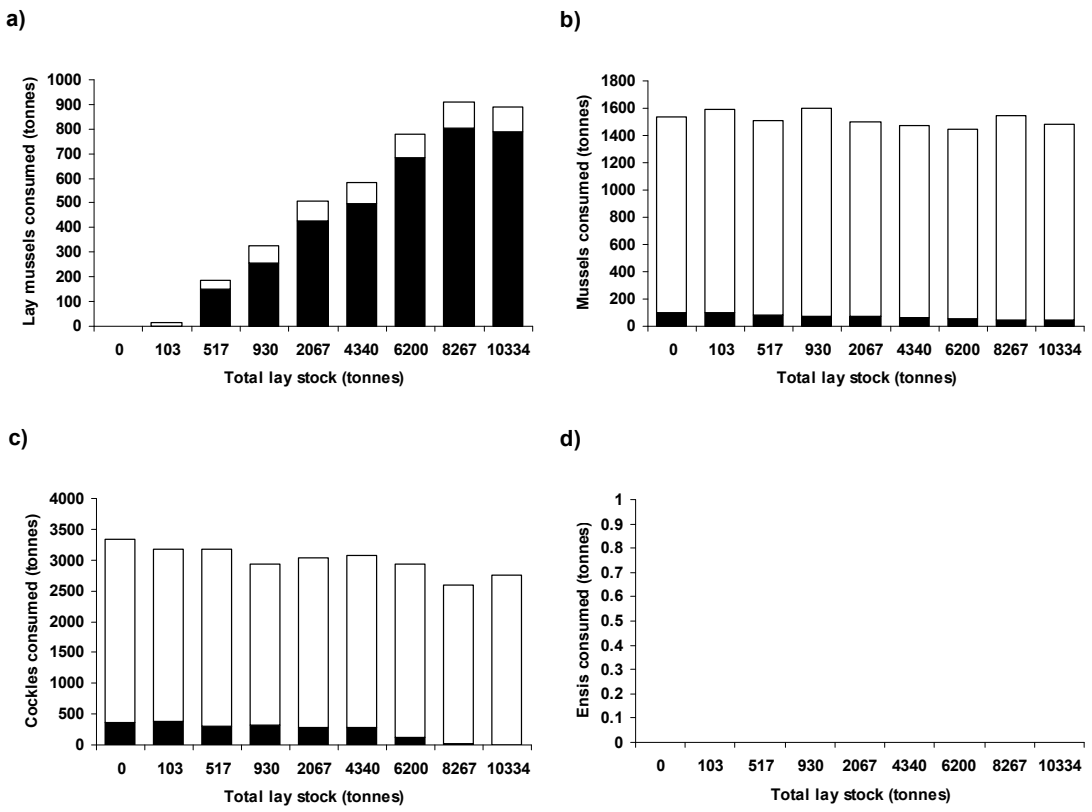

Figure 6.6 Total tonnage of shellfish removed overwinter from each of the four principal resource stocks by eiders (solid bars) and oystercatchers (open bars) as the total tonnage of lay mussels is reduced from the present day value of c 10,000t in a series of steps by gradually reducing the area and then removing lays in sequence as described in Table 4.1. a) Lay mussels, b) Regulated mussels, c) Cockles, d) *Ensis*. Background resource levels of cockles and regulated mussels are assumed to be medium and *Ensis* to be low ie Scenario 4 (see Table 4.2 for details of the values used). Note the different scales of the y axes shown in these figures.

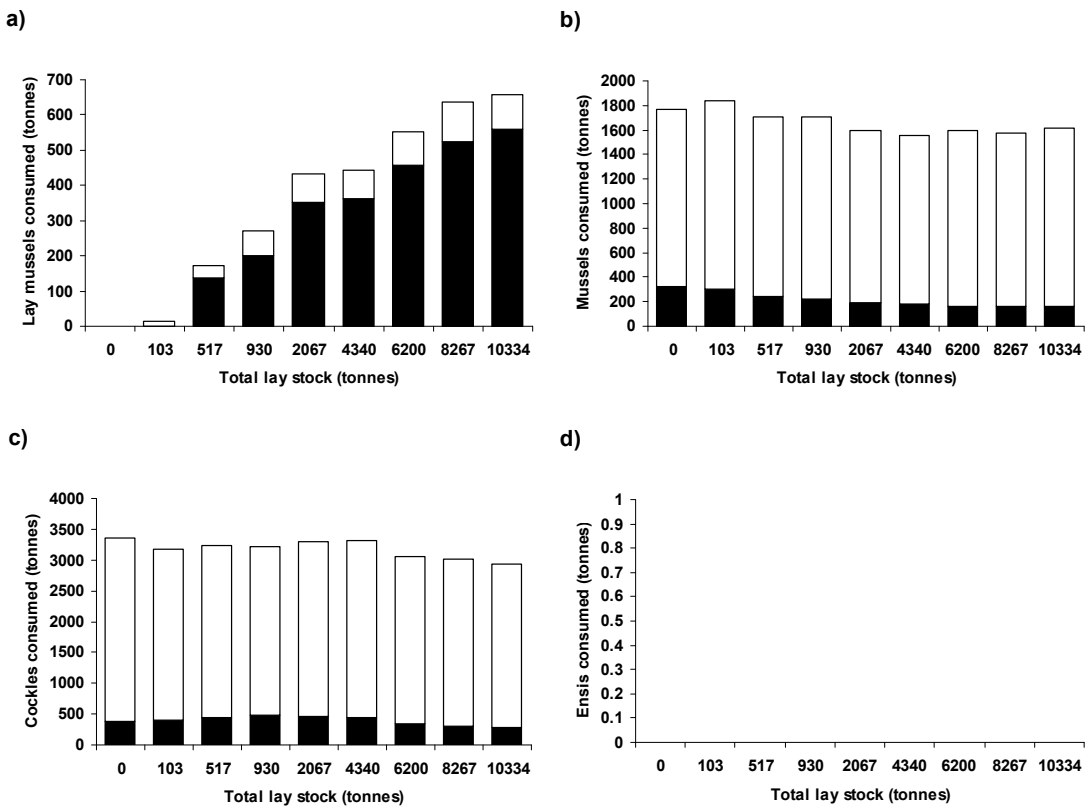

Figure 6.7 Total tonnage of shellfish removed overwinter from each of the four principal resource stocks by eiders (solid bars) and oystercatchers (open bars) as the total tonnage of lay mussels is reduced from the present day value of c 10,000t in a series of steps by gradually reducing the area and then removing lays in sequence as described in Table 4.1. a) Lay mussels, b) Regulated mussels, c) Cockles, d) *Ensis*. Background resource levels of cockles and regulated mussels are assumed to be high and *Ensis* to be low ie Scenario 5 (see Table 4.2 for details of the values used). Note the different scales of the y axes shown in these figures.

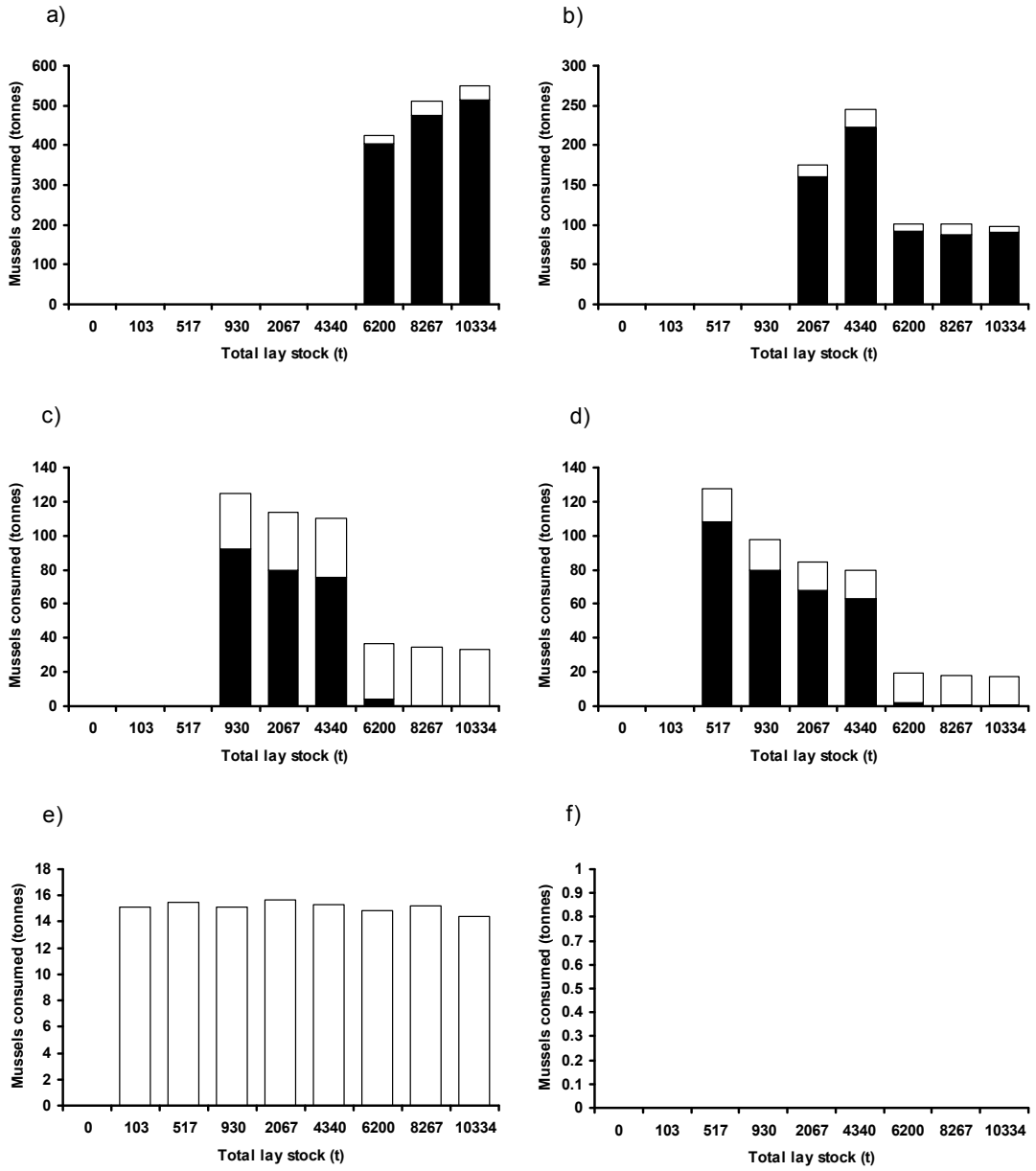

Figure 6.8 Total tonnage of mussels removed overwinter from each of the six principal lays by eiders (solid bars) and oystercatchers (open bars) as the total tonnage of lay mussels is reduced from the present day value of c 10,000t in a series of steps by gradually reducing the area and then removing lays in sequence as described in Table 4.1. Losses are shown separately for a) Roger, b) Toft, c) Clay Hole, d) Scotsman's Sled, e) Black Buoy and f) Herring Hill. Background resource levels of cockles and regulated mussels are assumed to be medium and *Ensis* to be high ie Scenario 1 (see Table 4.2 for details of the values used). Note the different scales of the y axes shown in these figures.

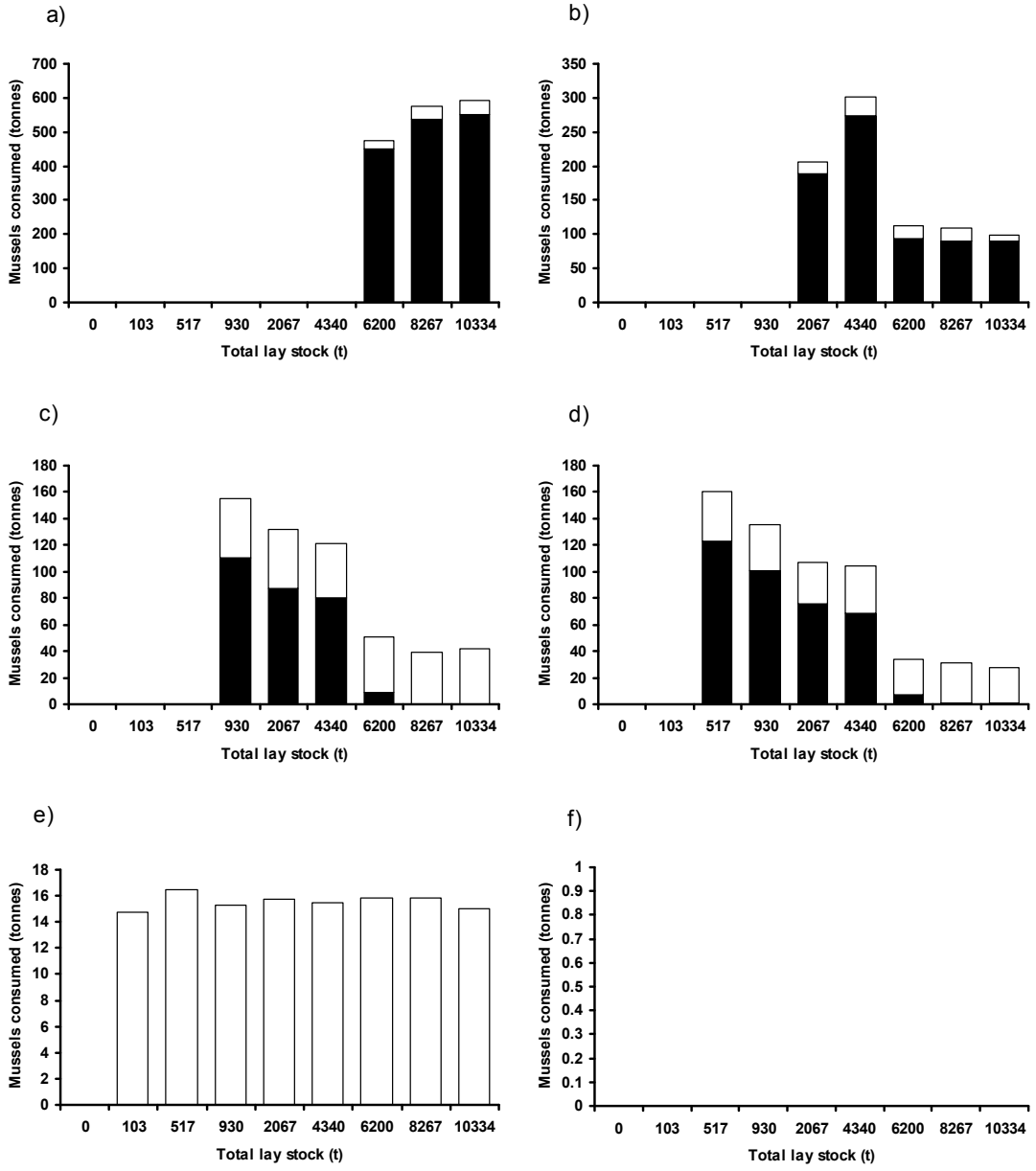

Figure 6.9 Total tonnage of mussels removed overwinter from each of the six principal lays by eiders (solid bars) and oystercatchers (open bars) as the total tonnage of lay mussels is reduced from the present day value of c 10,000t in a series of steps by gradually reducing the area and then removing lays in sequence as described in Table 4.1. Losses are shown separately for a) Roger, b) Toft, c) Clay Hole, d) Scotsman's Sled, e) Black Buoy and f) Herring Hill. Background resource levels of cockles and regulated mussels are assumed to be low and *Ensis* to be high ie Scenario 2 (see Table 4.2 for details of the values used). Note the different scales of the y axes shown in these figures.

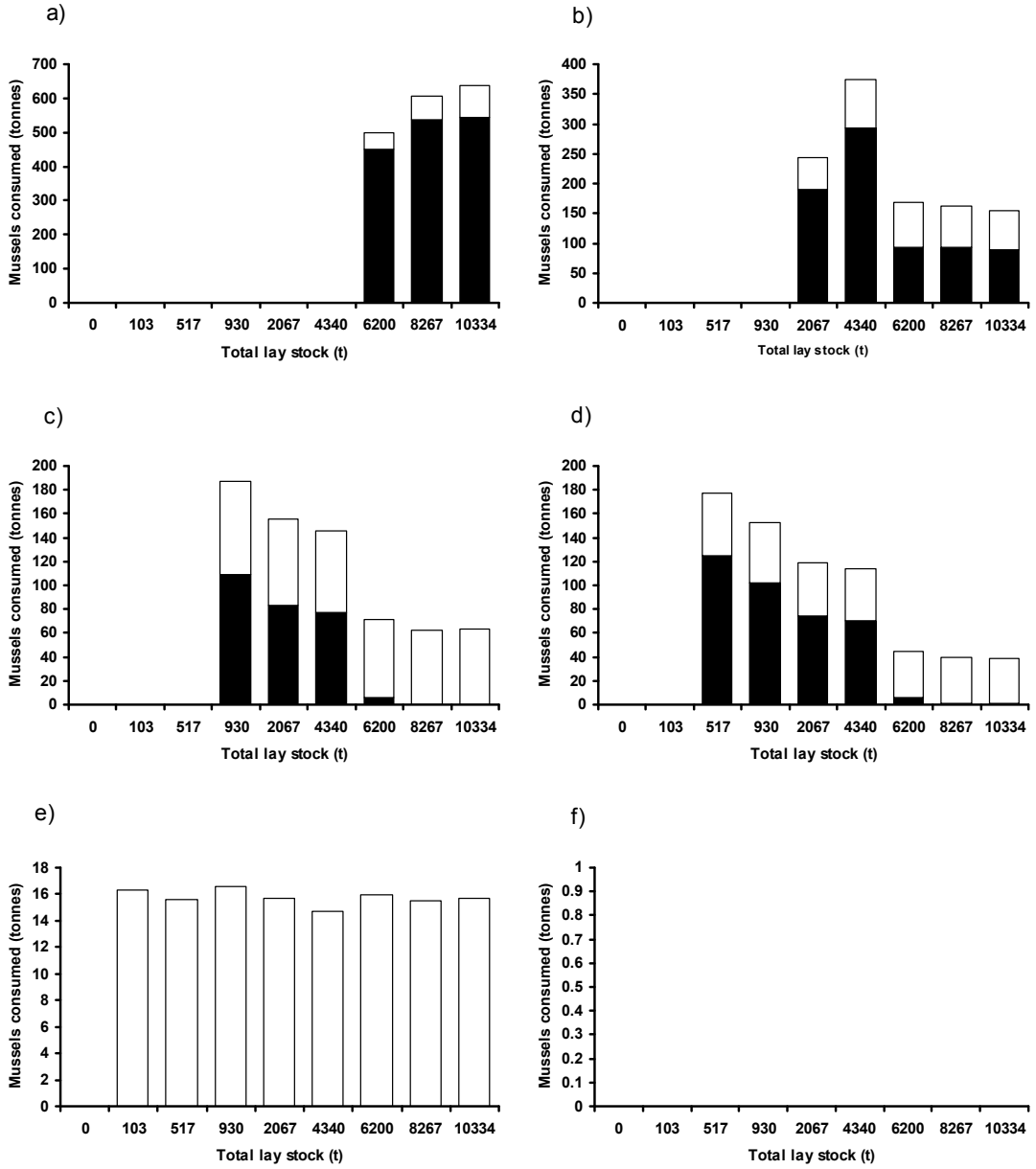

Figure 6.10 Total tonnage of mussels removed overwinter from each of the six principal lays by eiders (solid bars) and oystercatchers (open bars) as the total tonnage of lay mussels is reduced from the present day value of c 10,000t in a series of steps by gradually reducing the area and then removing lays in sequence as described in Table 4.1. Losses are shown separately for a) Roger, b) Toft, c) Clay Hole, d) Scotsman's Sled, e) Black Buoy and f) Herring Hill. Background resource levels of cockles and regulated mussels are assumed to be very low and low respectively while *Ensis* is assumed to be high ie Scenario 3 (see Table 4.2 for details of the values used). Note the different scales of the y axes shown in these figures.

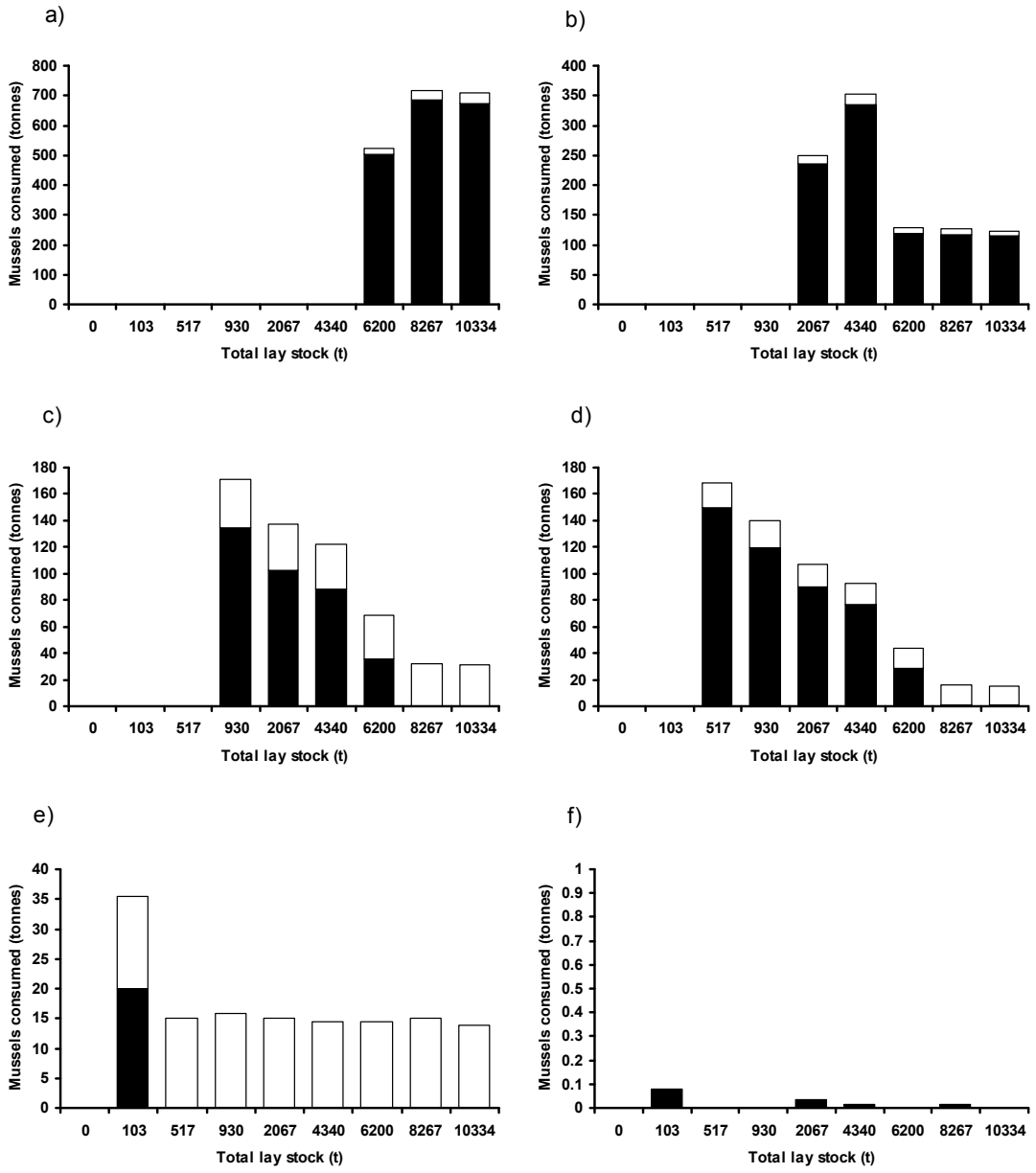

Figure 6.11 Total tonnage of mussels removed overwinter from each of the six principal lays by eiders (solid bars) and oystercatchers (open bars) as the total tonnage of lay mussels is reduced from the present day value of c 10,000t in a series of steps by gradually reducing the area and then removing lays in sequence as described in Table 4.1. Losses are shown separately for a) Roger, b) Toft, c) Clay Hole, d) Scotsman's Sled, e) Black Buoy and f) Herring Hill. Background resource levels of cockles and regulated mussels are assumed to be medium and *Ensis* to be low ie Scenario 4 (see Table 4.2 for details of the values used). Note the different scales of the y axes shown in these figures.

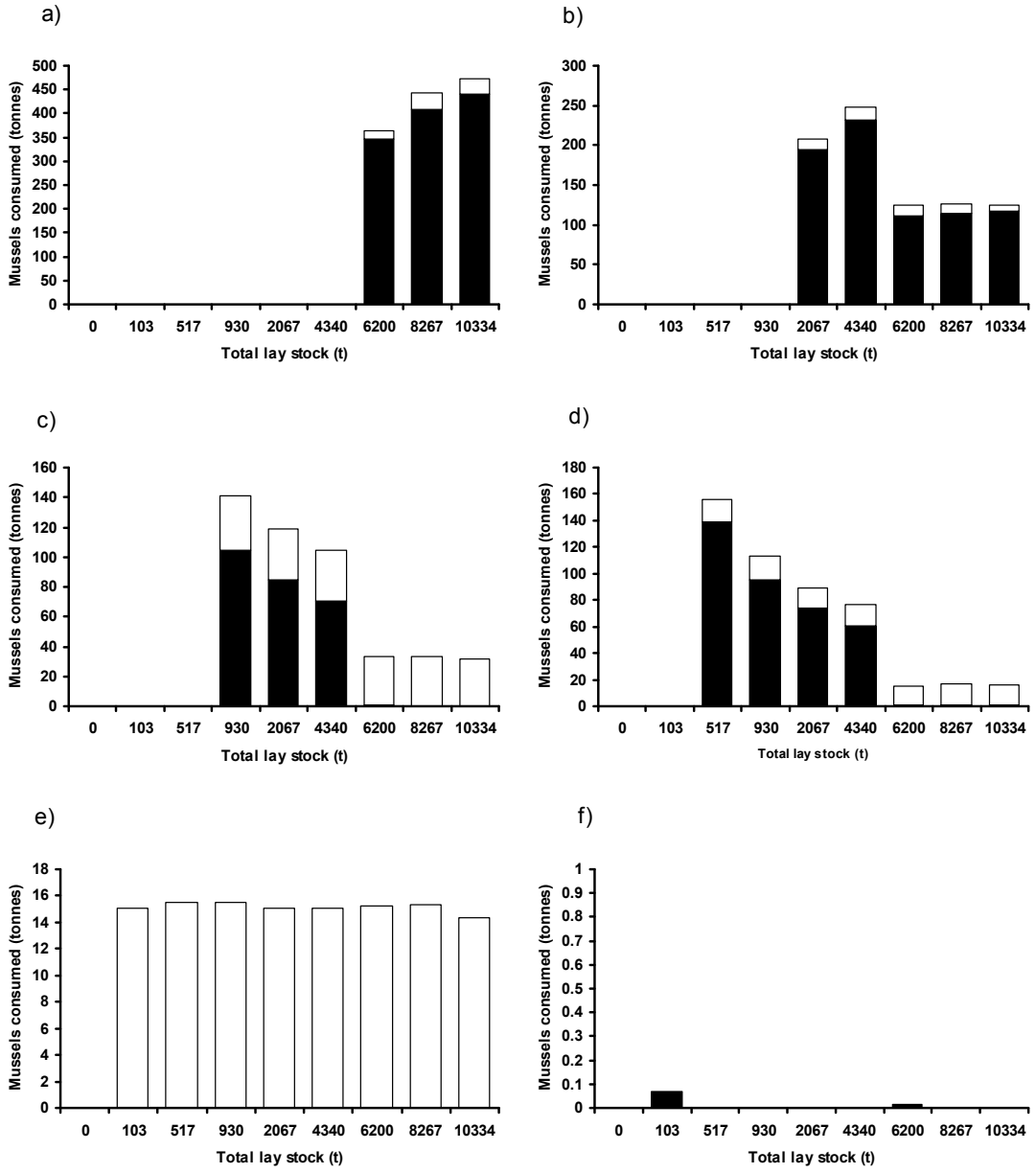

Figure 6.12 Total tonnage of mussels removed overwinter from each of the six principal lays by eiders (solid bars) and oystercatchers (open bars) as the total tonnage of lay mussels is reduced from the present day value of c 10,000t in a series of steps by gradually reducing the area and then removing lays in sequence as described in Table 4.1. Losses are shown separately for a) Roger, b) Toft, c) Clay Hole, d) Scotsman's Sled, e) Black Buoy and f) Herring Hill. Background resource levels of cockles and regulated mussels are assumed to be high and *Ensis* to be low ie Scenario 5 (see Table 4.2 for details of the values used). Note the different scales of the y axes shown in these figures.

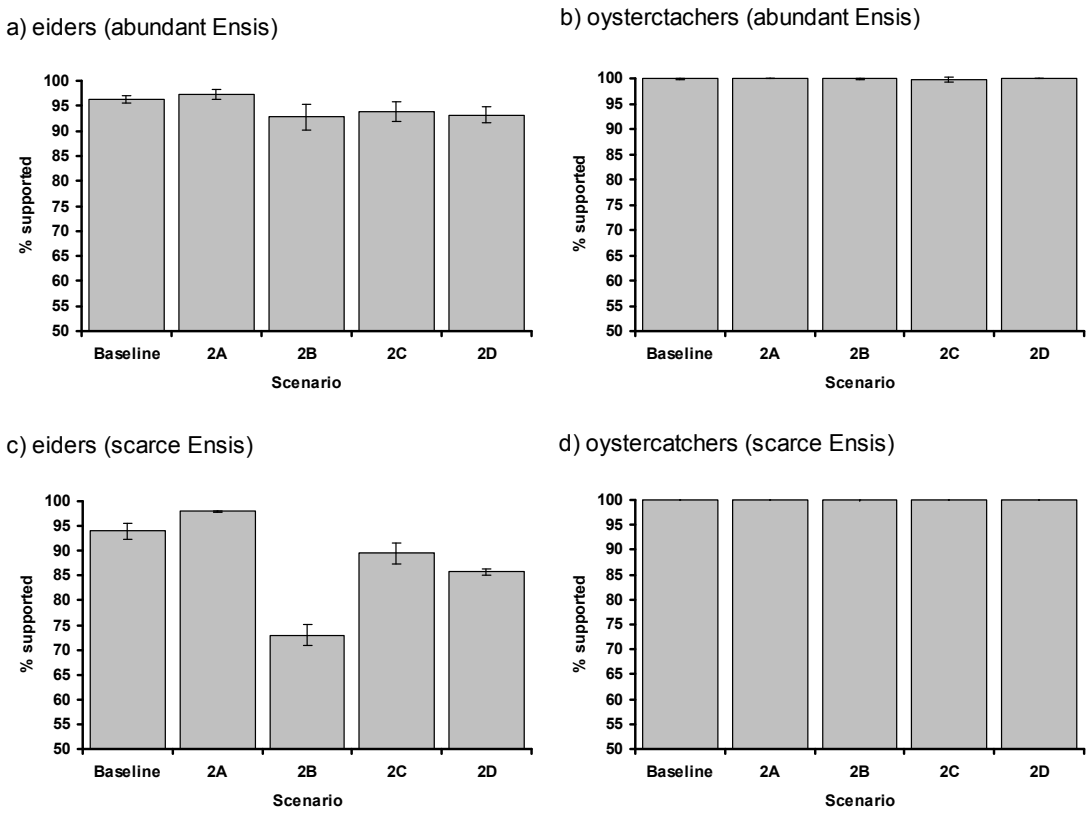

Figure 6.13 Predicted percentages of the populations of eiders and oystercatchers that are supported under various scenarios between which the distribution of the stock of lay mussels differs (see Table 4.3 for details). Each bar represents the mean predicted percentage averaged across 3 replicate simulations. Error bars denotes +/- 2se. In all plots, the stocks of cockles and mussels on the regulated beds are taken to be as they are today. In a) and b) the stock of *Ensis* is set at 10,000t. In c) and d) the stock of *Ensis* is set at 1,000t.

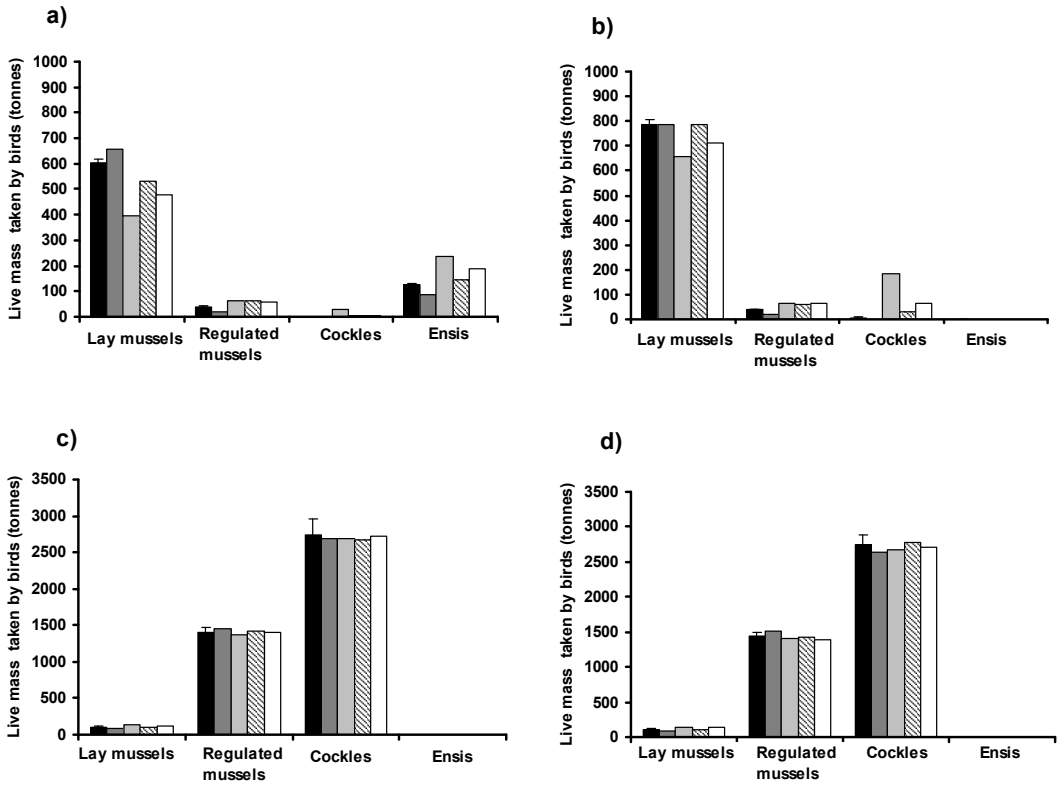

Figure 6.14 Total tonnage of shellfish removed over winter by eiders (a & b) and oystercatchers (c & d) from each of the four principal shellfish resources given various alternative ways in which the current total stock of lay mussels is distributed (baseline – black, scenario 2a – dark grey, scenario 2b – pale grey, scenario 2c – hatched, scenario 2d open) (see section 4.2.2 for details). In a) and c) the background shellfish resource levels are as today whereas in b) and d) the *Ensis* stock is assumed to have returned to a low level (1,000t). For the baseline scenario the error bars denote +2se around the mean averaged over five replicate simulations. Note the different scales of the y axes shown in these figures.

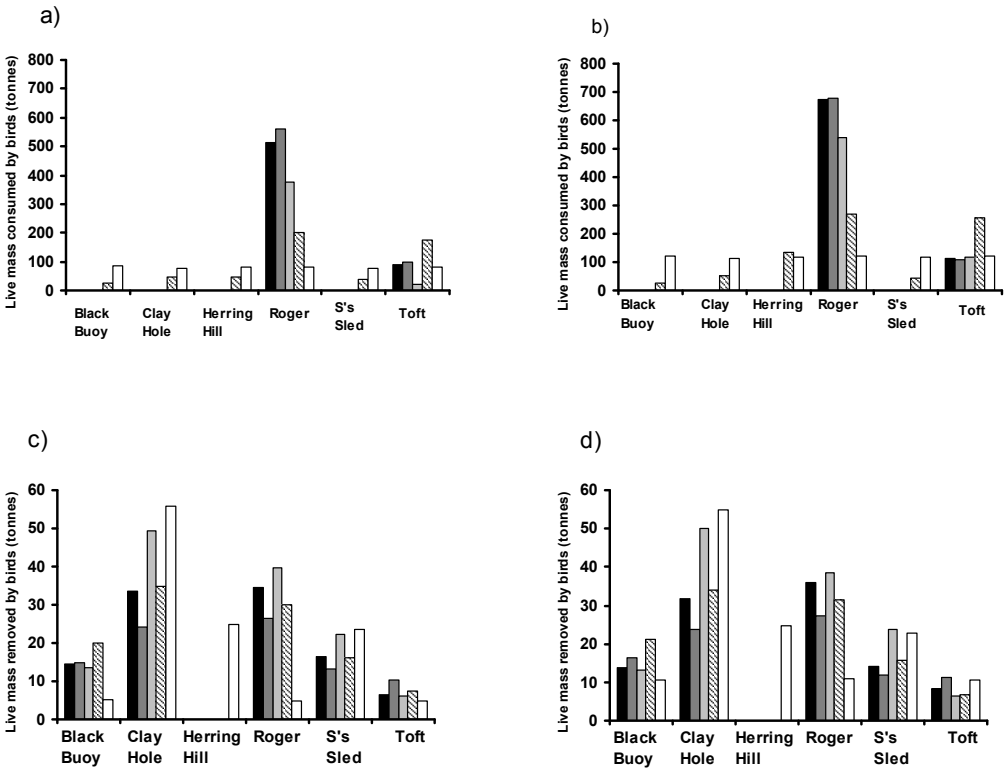

Figure 6.15 Total tonnage of mussels removed over winter by eiders (a & b) and oystercatchers (c & d) from each of the six principal lays given various alternative ways in which the current total stock of lay mussels is distributed (baseline – black, scenario 2a – dark grey, scenario 2b – pale grey, scenario 2c – hatched, scenario 2d open) (see section 4.2.2 for details). In a) and c) the background shellfish resource levels are as today whereas in b) and d) the *Ensis* stock is assumed to have returned to a low level (1,000t). Note the different scales of the y axes shown in these figures.

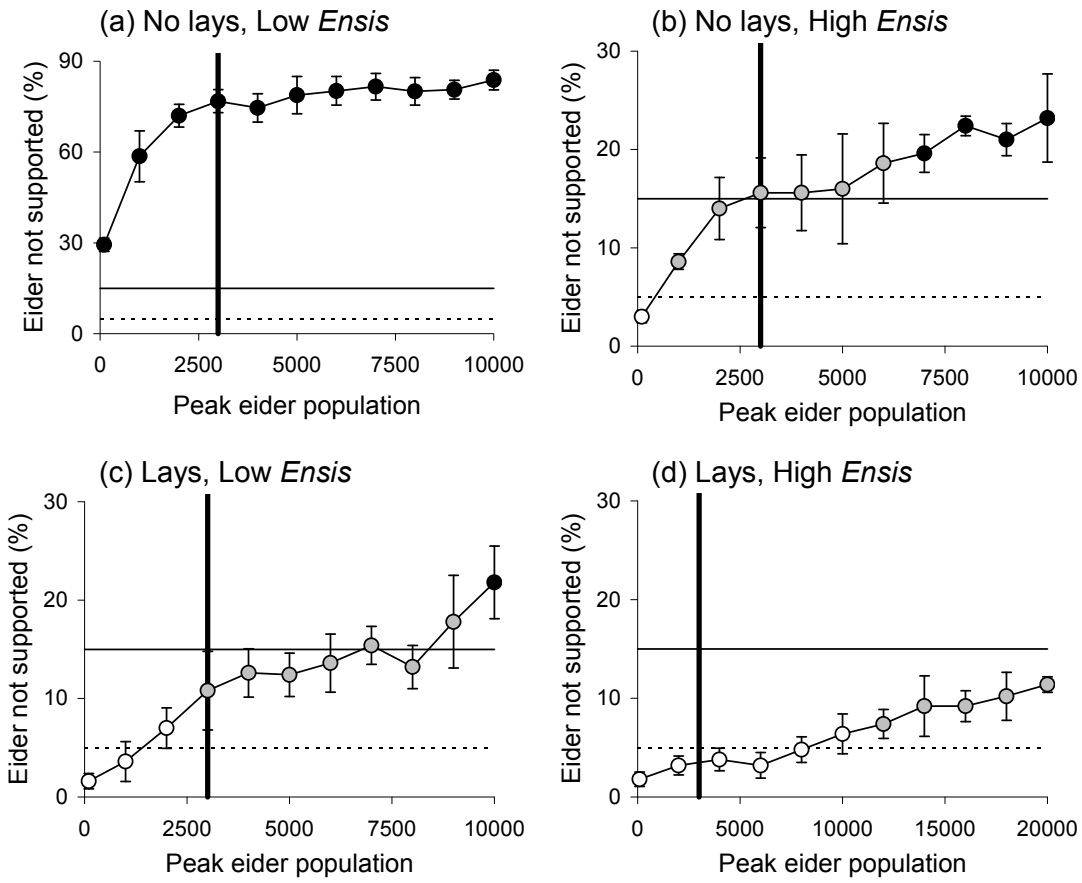

Figure 6.16 Relationship between the predicted percentage of the eider population that is not supported by the shellfish stocks within The Wash and the size of the peak population of eiders attempting to settle in The Wash in the winter under four differing shellfish resource scenarios. Each point depicts the mean (+/- 2se) percentage not supported averaged across five replicate simulations. Open symbols indicate those population sizes at which the mean predicted percentage not supported is not significantly greater than a value of 5 per cent. Grey shaded symbols indicate those population sizes at which the mean predicted percentage not supported is significantly greater than a value of 5 per cent. Black shaded symbols indicate those population sizes at which the mean predicted percentage not supported is significantly greater than a value of 15 per cent. The threshold value of a 'typical' overwinter mortality of 5 per cent is shown by the dotted horizontal line. The upper threshold value of an 'exceptional' overwinter mortality of 15 per cent is shown by the solid horizontal line. In each graph the solid vertical line depicts the current peak eider population of 3,000 birds.

Appendices

All of the references listed in the column ‘source’ are given in full in the bibliography to the report. References to ‘Approp Assess 2005’ in these appendices refer to the Record of Appropriate Assessment under Regulation 48 of the *Conservation (Natural Habitats &c.) Regulations* 1994 prepared by English Nature and are listed in the bibliography as ‘English Nature (2005)’. References to ‘Goss-Custard notes’ refer to unpublished notes made by Dr John Goss-Custard which are not listed in the bibliography. Text presented in the column headed ‘comments’ is largely taken directly (but not necessarily verbatim) from the source reference. However, some of the comments have been written by RWGC and not by the authors of the source paper. Therefore, any reader wishing to quote from the source reference is advised to refer to the original source paper first. References mentioned in the column headed ‘comments’ are those cited by the source reference and are not necessarily included in the bibliography to this report, unless they are also a source document elsewhere in the appendices.

Appendix 1 Notes concerning the foraging behaviour of diving ducks

source	species	parameter	comments
Approp Assess 2005	common eider	foraging timing	Eider on The Wash have been observed roosting on the flats at low tide (Yates pc)
Approp Assess 2005	common eider	foraging timing	Based on this information, we consider that eider are only feeding when the beds/lays are submerged
Approp Assess 2005	common eider	habitat choice	Assume that 0-2m above chart datum represents the eiders' preferred feeding grounds (based on observed distribution)
Ball 1990	canvasbacks	prey selection	canvasbacks thus selected prey at the level of individual food items. They rejected non-preferred prey probably because of a digestive constraint. They incur an opportunity cost (of eating a low quality item) because of the inability to later ingest a high quality item if one is found because the digestive tract is full. In general then, an optimally behaving omnivore should eat all foods encountered unless eating food 2 prevents it from eating food 1 by contributing to a bottleneck in digestion. Linear programming approaches (eg Belovsky 1984) emphasises the nutritional differences between prey as well as the digestive constraints on the predator (unlike classical optimal foraging theories that emphasises the importance of search and handling time but typically ignore differences between prey other than their yield of energy per unit time (Pyke 1984). It is probably no coincidence that the optimal foraging approach has had success predicting the diet of carnivores whereas the other approach has proven highly successful with herbivores (This latter approach would probably apply equally apply to carnivorous ducks that ingest hard-shelled prey whole and which risk filling up with low quality indigestible prey if they do not select individual prey items.)
Ball 1990	canvasbacks	touch/visual	canvasbacks are omnivores that dive and search for prey using tactile cues.
Ball 1990	pochard	touch/visual	touch (Suter 1982 in Draulans 1987)

Beukema & Cadee 1996	oystercatchers	giving up densities	..or cockles which were hardly present in beds of sufficient density to be profitably exploited by oystercatchers (Horwood and GC 1977: about 50 per sq m). THEREFORE THE USE OF 10 PER SQ M TO DEFINE THE OUTER LIMITS FOR THE COCKLE BED SURVEYSOF THE WASH WILL INCLUDE ALL OF THE USEABLE AREA AND THEN SOME BUT MAY REDUCE THE BED WIDE AVERAGE DENSITY BELOW THAT OF THE TRUE AREA UTILISED BY THE BIRDS
Beukema 1993	oystercatchers	giving up densities	Threshold densities below which oystercatchers cannot profitably feed on PURE stands of cockles appear to be close to about 50 big cockles per sq m (Horwood & GC 1977, Swennen pers comm).
Beukema 1993	oystercatchers	giving up densities	The extreme depletion of cockles observed in 1990/91 is remarkable in view of the widely accepted existence of threshold densities below which foraging is impossible. Such threshold densities may often have been overestimated because a) birds may leave an area long before they reach the lowest threshold and b) birds may not always work with maximal effort. As long as the TOTAL prey density is above the threshold for profitable feeding (on all prey mixed) I expect that the prey most preferred or easiest to track can be depleted to close to zero levels. This may have been the case in particular with cockles on Balgzand in 1990/91. A sharp threshold in cockle density might be absent if there is sufficient alternative prey in the same area.
Beukema 1993	common eider	numerical response	the consequences of the coinciding low stocks of mussels and cockles in 1990/91 were dramatic for the eider population wintering in the Dutch Wadden Sea: they concentrated on the last mussel banks present ie the culture lots, where they were regularly chased away. A significant proportion left the area or died (refs)
Bourne 1984	scoters	depth of prey	all three species of scoters ingested food organisms directly OFF THE BOTTOM, this feeding habit was most prevalent in black (common) scoters) White-winged and surf scoters DUG ACTIVELY IN THE SOIL AND FED MORE EXTENSIVELY ON BURIED CLAMS. Possibly because ww scoters are larger birds they are able to dig deeper and feed more extensively on littleneck clams (down to 15cm) than the other two spp of scoter

Bourne 1984	scoters	depth of prey	horse clams in the upper 10cm of the soil may have been buried too deeply to be an important food of scoters
Bourne 1984	scoters	habitat choice	ducks were feeding primarily in the intertidal zone. Scoters probably feed on intertidal beaches because of the shallow depths and the abundance of preferred food organisms. Bourne 1984
Brager et al 1995	common eider	foraging efficiency	for immature seaducks this might mean that their diving abilities are not yet fully developed to compete with the adults for food in deeper water. Eiders less able to compete successfully were probably seeking the (coastal) habitat offering a stable but less profitable intake (than offshore) to improve their survival probability. This could be compared to the results of Guillemette et al 1992 who found that individual eider feeding in small flocks were in bad condition compared to individuals feeding in large flocks.
Brager et al 1995	common scoter, eider and l.t.duck	habitat	in offshore shallow waters you get large seaduck concentrations until Jan, which later disappear. The much smaller flocks feeding in the coastal shallow waters stay there throughout the winter (source Brager et al 1995)
Brager et al 1995	common scoter, eider and l.t.duck	habitat	the densities of each of the three seaduck spp in offshore shallow waters are more than 11 times higher than those in coastal shallow waters (source Brager et al 1995)
Brager et al 1995	common eider	habitat	decrease in numbers in late winter due to abandonment of shallow reef areas with previously high densities of mussels
Brager et al 1995	common scoter	habitat	scoters seem to prefer to use offshore shallow waters rather than coastal shallow waters in the German Baltic (source Brager et al 1995)
Brager et al 1995	common eider	numerical response	WE hypothesise that the carrying capacity of shallow waters is strongly limited by the food resources due to consumption or hydrodynamic abrasion possibly reinforcing each other
Brager et al 1995	common eider	numerical response	The decrease in eider and ltduck numbers in the early winter suggests that the carrying capacity is limited by factors hampering the persistence and accessibility of the benthic food stock and NOT BY ITS SEASONAL MAXIMUM

Campbell 1978	common eider	foraging mode	three feeding techniques were observed. Dabbling, including up ending and crater feeding (as described by Player 1971) occurred mainly on the ebb tide and at low tide when areas of the mussel bed were exposed. Diving occurred throughout the tidal cycle but least frequently around low tide. The third technique (raft-feeding) involved high intensity synchronised or progressive DIVING amongst tight rafts of eiders. This occurred in the late afternoon and at dusk preceding departure of the flock from the study area.
Campbell 1978	common eider	foraging mode	Crater feeding was infrequent and involved only small numbers of birds at the lowest states of the tide
Campbell 1978	common eider	foraging timing	peaks in feeding intensity were evident on the ebb tide and around low tide and also, regardless of the tide, towards dusk.
Campbell 1978	common eider	foraging timing	..although flocks of several hundreds regularly fed on the mussel beds at the mouth of the Esk around low tide….
Campbell 1978	common eider	foraging timing	the existence of tidal routines in the Ythan and Tay would appear to be the product of the specialised hydrological characteristics of confined estuarine areas.
Campbell 1978	common eider	foraging timing	tidal differences in the relative availability of food during the day are probably insufficient to alter the basic DIURNAL routine in open marine sites, the more extreme conditions within estuaries may make it difficult for feeding at certain states of the tide so that diurnal routines are replaced by tidal ones
Campbell 1978	common eider	movements	..it seemed that once eiders had reached alternative daytime feeding areas (other than Leith) there was no advantage in subsequently moving to Leith when low tide occurred later in the day. BUT, once they had fed around low tide at Leith many flighted eastwards suggesting a preference for these other areas later in the day or at other states of tide
Camphuysen et al 2002	common eider	habitat choice	Swennen et al (1989) had indicated that eiders obtained c20% of their prey from mussel culture lots, but since the early 1990s the significance of mussel cultures for wintering eiders has increased markedly (Baptist et al 1997, Berrevoets et al 2000)

Carbone & Houston 1994	pochard	habitat choice	when offered two options the birds changed their mean preference from a patch with higher food density to one with a lower food density as the depth of the higher density patch was increased. However, they switched their preference earlier than expected based on estimates of the net rates of gain. This suggests that FACTORS OTHER THAN ENERGETICS INFLUENCE THE CHOICE OF FORAGING AREAS. it is possible that there are certain risks involved in diving at greater depths which offset the otherwise greater energetic profitability of deeper patches in the expts.
Carbone 1995		habitat choice	at present we have a very poor understanding of how substrate conditions influence feeding site preferences
Cramp & Simons vol 1 1977	common scoter	habitat	shallow inshore waters,
de leeuw 1997	diving ducks	food density	the fine grain or first order patchiness of the food supply as perceived by the ducks could not be exactly assessed because bottom samples with a VV grab (0.04 sq m) cover a much smaller area than a diving duck can scan in a single dive. (at least 1 sq m). Therefore diving ducks may perceive a more homogeneous distribution of mussels than expected from the variation in bottom samples. Hence considering larger scale variation at the level of patches is more appropriate for diving ducks.
de leeuw 1997	tufted duck/pochard	giving up densities	diving ducks apparently adjust their foraging effort at the level of patches with respect to the relative benefit of the patch in relation to that of the environment generally,.
de leeuw 1997	tufted duck/pochard	giving up densities	The giving up density is likely to be determined by the average food density of the site (several km2) and local food QUALITY. In such a system, the relatively scarce rich patches will be underexploited.
de leeuw 1997	scaup	numerical response	In lake Ijsselmeer the number of scaup bird days in a 2x2km grid cell correlated best with biomass in those grid dells where the probability of encountering mussels was at least 70% (ie >=7 out of 10 grab samples contained mussels). If cells with lower probabilities were included, the relationship between bird days and cell biomass becomes weaker. Similarly, the number of scaup correlated well with the number of grid cells within an area that meet the profitability criteria of sufficiently high biomass (ie above the threshold density of 50gfw/sqm) and shallow depths

de leeuw 1997	scaup	numerical response	…these authors attributed deviations from model predictions mainly on shortcomings in an adequate assessment of patchiness of the food supply.(Lovvorn 1994b, Lovvorn & Gillingham 1996)
de leeuw 1997	tufted ducks/scaup	patch quality	Also, the probability of finding food (ie its patchiness as opposed to fine scale density) both at the level of patches and of larger units of profitable area for feeding flocks seems an important criterion for habitat selection. Sampling programs of patchiness at levels relevant to diving ducks linked to field measurements of foraging effort and habitat use of individual birds could further enhance our understanding of where and how diving ducks can forage profitably
de leeuw 1997	tufted ducks/scaup	patch quality	the condition of mussels proved to be an important criterion for the profitability of foraging sites. Investigations of depth-dependent and local variations in mussel condition could further improve our insight to what extent exploitation by diving ducks is limited.
de leeuw 1997	diving ducks	patch use	areas with highly profitable mussels received more attention from the ducks, which could be ascertained at various levels of scale: lake, region, site and patch,. Size selection only operated at shallow depths indicating a time constraint on the ducks set by water depth.
de leeuw 1997	diving ducks	patch use	there is a trade off between the costs of commuting flights and the profitability of a certain foraging site
de leeuw 1997	diving ducks	patch use	during daytime the ducks aim to minimise extra energy costs for maintenance.
de leeuw 1997	tufted duck/pochard	patch use	we showed under use of some rich patches. This is probably due to imperfect knowledge of the environment (night time foraging underwater).
de leeuw 1997	tufted duck/pochard	patch use	The choice of a certain foraging area by a flock of several thousand birds is probably influenced by the average quality of the site rather than by peak densities which only a limited number of birds will experience in a patchy envt.
de leeuw 1997	tufted duck/pochard	patch use	patch exploitation by individual birds is subservient to the flock's attendance to a site.

de leeuw 1997	tufted duck/pochard	patch use	the results indicate that the ducks are not only able to recognise and to respond to differences in mussel density, but also to different quality over short distances
de leeuw 1997	tufted duck/pochard	patch use	diving ducks seem to choose their foraging and roosting sites from the perspective of MINIMISATION OF ENERGY COSTS FOR TRANSPORT (SHORT FLIGHT TRACKS AND COSTS FOR EXTRA LOCOMOTION AT THE ROOST.. Secondly, individual decisions are made with respect to the exploitation at the level of patches and sites WITHIN A REGION. These decisions are apparently taken from the perspective of MAXIMISATION OF ENERGY INTAKE.
Degraer et al 1999	common scoter	habitat	possibly a combination of food availability and the lack of disturbance, by fishing activities for instance, determines their spatial distribution
Dunthorn 1971	common eider	foraging timing	Bent (1925) and Marriott (1966) found that eiders fed twice every 24 hours and that the times of peak feeding activity coincided with LOW WATER. This contrasts with the daily rhythm with peak feeding activity at morning and evening at Linne Mhuirich.
Fox 2003	both species of scoter	foraging mode	some diving ducks are known to probe and dig in soft substrates for single food items (suter 1982, ball 1990) and it seems likely that scoter may use this feeding technique, especially for prey items towards the upper end of the size spectrum selected.
Fox 2003	both species of scoter	foraging mode	Long-tailed duck are thought to strain small (<16mm) prey items from sediments…This is thought to be a common filtering technique used by many benthic feeding diving ducks to sift small prey items, perhaps including scoter.
Fox 2003	both species of scoter	foraging mode	we lack even the most rudimentary understanding of how these birds feed
Fox 2003	both species of scoter	habitat	if we are to make the simplest predictions of where, when and in what numbers moulting and wintering scoter occur in relation to their food supply, we need to understand a great deal more about their basic foraging ecology and behaviour and their prey
Fox 2003	scoters	habitat	there is more to habitat selection than just benthic community and sediment type
Fox 2003	common scoter	habitat choice	common scoter favour feeding on areas of sandy bottom

Fox 2003	velvet scoter	habitat choice	a sandy substrate specialist (Madsen 1954)
Giles 1989	tufted duck(lings)	habitat choice	…demonstrates the ability of very young birds to locate and exploit small food patches within a novel environment over the course of a relatively few experimental replicates
Giles 1989	tufted ducklings	touch/visual	a combination of visual hunting and substrate probing with the tip of the bill was used to capture the molluscs
Giles 1990	tufted duck(lings)	foraging behaviour	it seems likely that both diving ducklings and adult diving ducks can respond rapidly to changes in the benthic invert food supply by concentrating their foraging over areas of the highest habitat quality
Giles 1990	tufted ducklins	touch/visual	whilst the ducklings were underwater they searched for food both VISUALLY and by very actively PROBING the gravel with the tip of the bill. Food items were apparently detected by TOUCH
Goudie & Ankney 1986	common scoter	feeding method	all species (scoter, eider, longtduck and harlequin have chisel shaped bills with a prominent curved nail at the tip suggesting they all are adapted primarily for "picking" epibenthos from the substrate
Guillemette & Himmelman 1996	common eider	habitat choice	we conclude from this that the most important factor explaining the distribution of eiders over the winter is patch size and food biomass
Guillemette & Himmelman 1996	common eider	habitat choice	the second assumption of the IDF model (ie that birds have an ideal knowledge of resource distribution) is bipartite since eiders should be able to discriminate between patches of different quality and at the same time be able to find the best patch. This is UNREALISTIC on a short time scale as it would require perfect knowledge about the location of the highest quality patches and of the factors associated with patch quality... We argue that although it is possible that eiders cannot find the best patch on a short term basis, we believe this is possible on a long-term scale (an entire winter). (However, with static benthic prey and the use of only three patches in this system it is hard to see how assessing patch quality on a short term basis would be difficult for them)
Guillemette et al 1992	common eider	energy balance	eiders may in some way minimise energy expenditure in order to decrease the energy gain required for energy balance (cf point made by de Leeuw chapter 8/9)

Guillemette et al 1992	common eider	habitat choice	We calculated the DAILY NET ENERGY INTAKE for eiders feeding in the three habitats. The net gain during a foraging cycle was obtained by multiplying the net gain for an average dive cycle (energy per average prey - energetic cost of diving, handling and pausing) by the number of dive cycles in a feeding bout and then subtracting the energy spent during the resting bout. Multiplying this by the number of FORAGING BOUTS possible in the time available yielded an estimate of the net daily energy gain
Guillemette et al 1993	common eider	habitat choice	a disproportionate number of flocks and individuals forage around SHALLOW reefs where the HIGHEST DENSITY AND BIOMASS of prey are found
Guillemette et al 1996	common eider	numerical response	distribution closely coincides with locations where prey densities are highest
Guillemette et al 1996	common eider	numerical response	Cumulative utilisation of most reefs was proportional to their surface area. This suggests that eiders tend to deplete each patch equally during the winter.
Hart & Brown 2006	common eider	foraging timing	eiders foraged during the LOW WATER period and not, as envisaged during high water. The eiders foraged on the proportion of the mussel beds that remained submerged during the low water period and selected mussels by head dipping and diving in the shallow water. During high water the eiders loafed on the water and aggregated into large flocks. These aggregations tended to occur close to where the bird foraged during low water.
Hart & Brown 2006	common eider	habitat choice	the eiders showed a strong preference to forage on the commercial leys and did not predate the unprotected natural mussel beds on the Gat.
Hart & Brown 2006	common eider	habitat choice	The Gat bed (natural) continued to be unexploited by eiders despite the loss of the mussel stock from the Roger lay and the disturbance on the Toft lays caused by the deterrents and the activities of the mussel farmers

Hart & Brown 2006	common eider	habitat choice	one reason the Gat beds was unpredated by eiders may have been because the mussels here lay on relatively higher ground than the lays. As a consequence, relatively few mussels would have remained submerged and been available to the eiders during low water. Furthermore, the mussels on this high-level bed were probably less profitable.
Kirby et al 1993	common scoter	habitat	usually associated with sandy coasts
Kirby et al 1993	velvet scoter	habitat	shallow sandy areas Cramp & Simmons 1977
Kirby et al 1993	common scoter	movements	No regular dawn or dusk movements have been described and it is presumed that they remain to roost in or close to their daytime feeding areas
Kirby et al 1993	common scoter	movements	At least some flocks appear to remain faithful to the same areas throughout the winter; even in the Moray Firth where there are at least three alternative sites in close proximity, there has been NO EVIDENCE of any regular interchange
Koffijberg et al 2001	common eider	numerical response	the size of the mussel beds is small and they comprise less than 10% of the overall area of the study sections. Nevertheless, on average 60% of the eider population in these sections can be found on these mussel beds during midwinter.
Koffijberg et al 2001	common eider	numerical response	these marked shifts in the distribution of eiders have been attributed to depletion of the eider's food, blue mussels and cockles. As a result, birds started to feed on Spisula subtruncata which occur in the coastal zone off the Wadden Sea islands
Larsen & Guillemette 2000	common eider	numerical response	In the case of sea ducks, temporal relationships to food abundance are in general poorly understood, and no studies have addressed the relationship between sea duck abundance and annual variation in food supply.
Larsen & Guillemette 2000	common eider	numerical response	Combining the data for the 2 sites, the interannual variation in eider densities were significantly positively correlated with the total benthic biomass as well as blue mussel biomass in the 0-6m depth range BUT NOT in the 6-12m depth range
Larsen & Guillemette 2000	common eider	numerical response	the considerable annual fluctuations in abundance of the benthic food supply at 0-6m depth was closely reflected in the interannual pattern of the abundance of common eiders.

Laubhan & Metzner 1999	stellers eider	foraging timing	Previous studies have documented that stellers eiders forage primarily within 2-3 hours of low tide and that surface feeding is the dominant foraging strategy.)refs). In contrast, synchronous diving was the preferred foraging strategy in our study and time spent foraging was similar at high and low tide
Leopold et al 2001	common eider	foraging mode	prey may be taken while the bird is walking on dry land or it may be taken while submerged at tens of metres
Leopold et al 2001	common eider	foraging timing	feeding on cockles seems to be restricted by the tidal cycle in that this prey is mainly taken when a little water is present on the feeding site
Lovvorn & Gillingham 1996	canvasbacks	decision rules used in model	if expected energy balance on a subsequent dive in the same locus was positive based on the functional response for the decremented food density and the energy cost of the preceding dive, the MODEL duck dove again. If not, the MODEL duck moved to another locus. Direction was assumed random and distance drawn at random from a field derived freq distribution
Lovvorn & Gillingham 1996		habitat	detailed mapping of benthic foods on a scale relevant to the foraging energetics of highly mobile birds is currently not feasible, despite the importance of food dispersion to their foraging profitability and sustainable population levels.
Lovvorn & Gillingham 1996	canvasbacks	habitat choice	waterfowl in the field did not find high density loci and deplete them disproportionately, but appeared to feed in all loci encountered with profitable food densities
Meissner & Brager 1990	common scoter	distribution	it has been proposed that their distribution in the Keil Bay primarily depends upon the depth of water and the zonation of the macrofauna
Mori & Boyd 2004	fur seal	foraging behaviour	diving time budgets were consistent with the hypothesis of rate maximisation of energy intake during dives
Mori & Boyd 2004	fur seal	foraging behaviour	it appears that rate maximisation operates at all scales and leads to a set of behaviours that can result in the maximisation of fitness across a wide range of environmental variability.
Mori & Boyd 2004	fur seal	habitat choice	using travel time (ascent and descent) and total dive time (below surface) we calculated an index of patch quality based upon the diving behaviours of the seals themselves

Mori & Boyd 2004	fur seal	numerical response	fur seals were able to adjust their behaviour to track highly variable prey distributions and densities
Mori & Boyd 2004	fur seal	patch quality	Variation in travelling time is caused by variation in patch depth and variation in bottom time for a given travelling time is caused by variation in patch quality as suggested by some authors (refs). The quality is measured in terms of the time spent at the bottom of the dive adjusted for dive depth, and we used this as a proxy for the net rate of energy intake during the bottom time.
Mori & Boyd 2004	fur seal	patch quality	Foraging condition is determined by three factors (i.e. patch quality such as prey density, depth of patch and density of patches)
Mudge & Allen 1980	common scoter	foraging timing	feeding activity for common scoter was lowest around high tide when the bivalve beds were most difficult to reach.
Nehls & Ruth 1994	common eider	numerical response	eiders may concentrate in flocks of several thousands on mussel culture lots
Nehls & Ruth 1994	common eider	numerical response	the proportion of eiders that utilise mussel cultures is relatively low. One average only 23% are found on or close to culture lots (but probably this is a far higher % than the % of the area covered by these lots)
Nehls & Ruth 1994	common eider	numerical response	the utilisation of mussel cultures by eiders relates to the amount and size structure of the mussels found in these places.
Nehls & Ruth 1994	common eider	numerical response	the proportion of wintering eiders found on or close to culture lots closely follows the proportion of mussels found on the cultures (out of the total stock in the system). In 1991 and 1992 when eider numbers on the cultures were exceptionally high, mussel stocks on the cultures were very high and natural stocks low (ie a positive numerical response at the scale of between beds). The total numbers of eiders in the Wadden Sea of SH and the proportion that utilises mussel cultures rather shows an inverse relationship (ie the mussel cultures must be the preferred habitat).

Nehls & Ruth 1994	common eider	numerical response	the length distribution of the mussels determines the suitability of mussel beds or cultures for eiders. The high proportion of eiders found on mussel cultures in 1991 and 1992 coincides with the subtidal mussel stock reaching a length preferred by eiders (30-55mm mostly), in contrast to 1990 when mussels on the cultures were small (8-28mm) and few eiders utilised these places. However, this situation is not consistent over all years. in 1988 and 1989 when the mussels on the cultures were of similar size as in 1991 and 1992, but natural stocks of mussels were higher than during 1991 and 1992, few eiders were seen on mussel cultures
Nehls & Ruth 1994	common eider	numerical response	no clear response of eider numbers to the recent increase in mussel culturing could be detected up to now (at the scale of the Schleswig Holstein)
Nehls 1989	common eider	foraging mode	cockles are mainly taken from tidal flats by trampling. Eider can however take cockles by diving as they do regularly in the Baltic Sea (refs)
Nehls 1989	common eider	foraging mode	Mussels are taken by diving at high tide when eider aggregate in large flocks over the mussel beds, both on subtidal and intertidal areas
Nehls 1989	common eider	foraging timing	in the Wadden Sea feeding takes place mainly during the rising and ebbing tide. At low tide, eider rest on exposed sandflats or on the water.
Nehls 1989	common eider	numerical response	…other studies have shown the available food to be the main factor regulating the number of eider (Pehrsson 1973, 1978, 1984)
Nehls 1989	common eider	numerical response	In the Wadden Sea no changes in numbers that could be related to fluctuations in the abundance of cockles or mussels have been found SO FAR, although counts have been made for more than 20 years
Nehls 1989	common eider	numerical response	Nehls et al (1988) showed that the number of eiders does NOT depend on mussel cultures
Nehls 1995	common eider	foraging technique	In winter the proportion of eiders foraging by head-dipping is influenced by the tide and is highest around low water. The proportion diving is greater at other states of the tide as it advances and recedes (Fig 7.3)
Nehls 1995	common eider	foraging technique	In summer, almost all foraging is done at low tide and is done by head dipping not diving Fig 7.4
Nehls 1995	common eider	foraging timing	on 3rd July 1992, all foraging was done during daylight low water period. Fig 7.1

Nehls 1995	common eider	foraging timing	numbers on the high water roost are highest when HW occurs early am and are lower if high water is later in the day
Nehls 1995	common eider	foraging timing	in winter the most active period for head-dipping is from 2-3h before to 2-3 hours after LW. In winter, eiders dive at all stages of the tide but less so when head dipping occurs over LW +/- 3h Fig 7.5 & 7.6
Nehls 1995	common eider	foraging timing	activity patterns were characterised by diurnal and tidal rhythms both subject to seasonal changes. Tidal rhythm was most prominent during all seasons with highest foraging activities at low tide when eiders may feed by head dipping at exposed mussel beds.
Nehls 1995	common eider	foraging timing	In early spring when days were still short, eiders were active at all stages of the tide but as days got longer feeding was restricted to low tide.
Nehls 1995	common eider	habitat choice	the utilisation of mussel cultures by eiders strongly correlated with the size-distribution of the culture mussels and the amount of mussels found on the cultures in relation to the natural mollusc stocks. Mussel cultures are estimated to provide on average 10-20% of the food of eiders
Nehls 1995	common eider	numerical response	The number of wintering eiders utilising the cultures varied in relation to the amount and size of the mussels present and the proportion of eiders on the cultures in winter ranged from 10% to 60%
Nehls 1995	common eider	numerical response	Numbers and distribution of wintering eiders clearly fluctuated in relation to changing mollusc stocks (at the scale of the whole Schleswig Holstein Wadden Sea). This is not true of moulting eider numbers however.
Nehls 1995	common eider	size selection strategy	the size selection for mussels exhibited by eiders is not consistent with simply maximising net energy gained. This would be achieved by simply taking the largest mussels because net energy gained (in kJ) increases exponentially with increasing mussel length. However, energetic utilization or efficiency (not quite sure how this is defined - either net energy gain/energy content of mussel OR energy gain/energy expended i.e. a proportion in both cases) is maximal at intermediate sized mussels and this is what eiders select. (Fig 5.15)
Nehls 2001	common eider	foraging mode	Bivalves are captured by head dipping or diving up to depths of 30metres
Nehls 2001	common eider	foraging timing	cockles are mainly taken by head dipping when the tide is low

Nehls et al 1997	common eider	foraging timing	eiders feed on the mussel beds at all stages of the tide, except when the mussel beds are completely exposed. Highest feeding activities are generally reached when water levels are suitable for head-dipping.
Nehls et al 1997	common eider	habitat choice	as shell thickness and flesh content are negatively correlated (Goss-Custard et al 1983), …. This is most likely to affect eiders which swallow whole mussels and rely on high quality mussels. Mussel beds with long exposure times are therefore unlikely to be attractive food sources for eiders.
Nilsson 1972	scoters	habitat choice	distance to land might also be an important factor in determining distribution eg in the scoters
Nilsson 1972		habitat choice	a flying flock is attracted to other ducks (on the sea)
Pedroli 1982	tufted ducks	distribution	…which are the main feeding and resting areas of the ducks because of the high density of Dreissena.
Phillips 1991	pochard	habitat choice	pochard prefer to feed in shallow water and can select prey rich areas, thus maximising their food intake whilst minimising their energy expenditure
Phillips 1991	pochard	habitat choice	the feeding areas were significantly shallower than the unused areas
Phillips 1991	pochard	habitat choice	both the numbers and dry weights of larval chironomids were, however, found to be significantly higher in the preferred feeding areas than in the rest of the lake.
Phillips 1991	pochard	habitat choice	the birds were selecting feeding habitat within the favoured depth range
Phillips 1991	pochard	habitat choice	chironomid numbers in the areas where pochard were feeding were significantly greater than in the rest of the Main lake. The mean numbers of larvae per sample in the feeding area was 61.3 compared to 47.2 in the unused areas ie a 17% difference was detected
Piersma & Camphuysen 2001	common eider	numerical response	camphuysen et al (MS) found a significant negative relationship between mussel stock and the proportion of eiders utilising the North Sea coastal waters. Since 1990 the use of Spisula in the North Sea has become a permanent feature
Piersma & Camphuysen 2001	common eider	patch quality	culture plots of more mature mussels (ie not seed which are too small to be profitable) are excellent feeding sites for eiders.

Raffaelli et al 1990	common scoter	foraging timing	eiders forage on the Ythan mussel beds for about 5.5 hours around the time of low tide (although individual birds may only feed for part of this period)
Richman & Lovvorn 2003	canvasbacks	foraging mode	canvasbacks which commonly feed on Macoma balthica in the winter generally did not excavate plant tubers in the field at depths >10cm (source Lovvorn 1989)
Ross 1983	common scoter	habitat	no flock was detected more than 10km from the coast
Schenkeveld & Ydenberg 1985	surf scoter	foraging mode	often surfaced with single or small clumps of mussels which usually required considerable handling and positioning before being swallowed whole.
Stott & Olson 1973	scoters	habitat	all three scoter species preferred sandy beaches to rocky headlands and there was a decreasing density of these species as the proportion of rocky substrate increased
Stott & Olson 1973	scoters	habitat	the type of foods present may be a primary cause for sea duck use of particular habitat types
Stott & Olson 1973	scoters	habitat	These highly productive bivalve areas concentrated scoters from September to May
Stott & Olson 1973	white-winged scoter	habitat	the razor clam Solen sicarius which is found on sandy or silty substrate made up the major portion of ww scoters diet Grosz 1966
Stott & Olson 1973		habitat	also found scoters off sandy beach areas in Maine and Connecticut Snow & Billard pers comm
Stott & Olson 1973		habitat	found several thousand scoters in a large shallow sandy bay in Labrador on several occasions during late July Snow pers comm
Swennen 1976	common eider	distribution	in winter, the eider clearly avoids the coast, only immature and sick ducks keep near the shore in winter in the Wadden Sea.
Systad & Bustnes 2001	stellers eider	feeding method	incidence of feeding was highest at low tide
Systad & Bustnes 2001	stellers eider	feeding method	stellers eiders increased their feeding effort, but also reduced feeding costs by reducing diving depth in midwinter cold weather
Systad & Bustnes 2001	common eider	high water/low water	in general, feeding is more likely to occur at low tide (several refs)

Systad & Bustnes 2001	stellers eider	touch/visual	the diet of stellers eiders consists of gastropods, bivalves and crustaceans (ref) <Much of the prey can probably be found in darkness, so vision may be of little importance
Systad et al 2000	common eider	habitat choice (state dependency)	individuals in poor condition employed a risk-prone feeding strategy in which they used a habitat where food was less predictable but had a higher energy content (crabs) (Guillemette et al 1992)
Tome 1988	ruddy ducks	foraging behaviour	these results provide quantitative support for the prediction that ruddy ducks maximise their rate of net energy intake while foraging.
Van Gils et al 2005a	red knot	habitat choice	Thus, the observed patch choices imply that the birds were maximising their INSTANTANEOUS RATES OF ENERGY ASSIMILATION (due to the agreement between observed distribution as a function of gizzard mass and that predicted by the Digestive Rate Model)

Appendix 2 Notes concerning the amount of time spent in various phases of the dive cycle

source	species	parameter	comment
Beauchamp et al 1992	common eider	dive duration	total dive duration and bottom time increase with depth. The fact that bottom time increases with depth can be readily explained by the MVT. As divers forage deeper, time spent travelling and energy cost increase. Consequently, the expected foraging gain that follows the end of a dive decreases with increasing depth. Animals must therefore increase time spent foraging with increasing depth in order to maximise expected foraging gain over the complete feeding bout.
Bevan et al 1992	tufted duck	dive duration	the dive durations of tufted ducks are proportional to the depth of the water.
Bustnes & Lonne 1997	common eider	dive duration (s)	dives of common eiders usually last 30-60 secs (Ydenebrg & Guillemette 1991, Beauchamp et al 1992)
Bustnes & Lonne 1997	king eider	dive duration (s)	wintering king eiders mostly dive for more than 90secs (Systad & Bustnes unpubl data)
Carbone & Houston 1994	pochard	foraging time (on bottom)	neither foraging time nor surface time was significantly affected by the density of food
Carbone & Houston 1994	pochard	foraging time (on bottom)	a novel prediction of the models is that foraging time (on the bottom) first increases and then decreases with increasing water depth. Initially as the water depth increases, the travel time increases and so the diver increases the size of its O2 stores to allow for more foraging time, in order to reduce the number of trips between the surface and the foraging site. As depth increases further and the diver approaches its max dive duration, foraging time must decrease to compensate for increasing travel time.
Carbone & Houston 1994	pochard	dive duration	increased significantly with depth
Carbone & Houston 1994	pochard	travel time	increased significantly with depth

Carbone & Houston 1994	pochard	foraging time (on bottom)	did not significantly change with increasing food concentration. So, scarcity of food did not necessitate longer time periods on the bottom even though the rate of feeding on the bottom was c three times lower at the low food density
Carbone & Houston 1994	pochard	foraging time (on bottom)	increasing sand depth significantly reduced time on the bottom
Carbone 1995	pochard	foraging time (on bottom)	increases with water depth until it approaches a maximum asymptote in deeper water
Carbone 1995	pochard & tufted duck	proportion of time spent feeding over the dive cycle (including surface time)	decreases with increasing water depth in two datasets (due to increases in travel time ascent and descent) and increased time spent on surface recovering
Carbone et al 1996	tufted duck/pochard	surface time	Interdive intervals up to 35secs may be considered to be within a bout. If > 35secs then this equals the end of a foraging bout.
Carbone et al 1996	tufted duck/pochard	foraging time (on bottom)	Mean foraging time was also highly correlated with water depth in both spp- but both significantly non-linear (tended to level off at c 3m)
Carbone et al 1996	tufted duck/pochard	surface time	in both spp were highly correlated with water depth and significantly non-linear, kicking up at 3.5-4m. This kick may indicate a decline in aerobic efficiency and a reliance on anaerobic respiration.
Carbone et al 1996	tufted duck	foraging time (on bottom)	tufties significantly reduced the time spent foraging in response to increasing sand depth. Consumption rates declined significantly as sand depth increased
Carbone et al 1996	tufted duck/pochard	surface time	increased significantly in response to decreasing water temperatures.
Carbone et al 1996	tufted duck	foraging time (on bottom)	Sand depth of the prey had a strong affect on rates of mealworm consumption. However, rates of consumption did not affect foraging times in the pochard (Carbone & Houston 1994) nor did intake rates have a significant effect on the predicted foraging times (in the model of Houston & Carbone 1992).

de Leeuw 1997	tufted duck	surface time	increases roughly in proportion with depth up to 3.5m and thereafter increases more rapidly. Such trends have been used to indicate a decline in aerobic efficiency and a reliance on anaerobic respiration.
de Leeuw 1997	tufted duck	surface time	surface time should increase with increasing underwater costs for all depths
de Leeuw 1997	tufted duck	foraging time (on bottom)	time spent foraging at the bottom increased with diving depth
de Leeuw 1997	tufted duck	foraging time (on bottom)	Wilson & Wilson (1988) regard diving birds as central place foragers and predicted that they should increase their foraging time under water at greater depths in order to use their dive time most efficiently. We suggest therefore that selectivity for small size classes increased with diving depth because in deeper dives more time was spent in taking small mussels in a run before a large one was picked up at the end.
de Leeuw 1997	tufted duck	foraging time (on bottom)	we assume that divers aim to maximise the proportion of time of the dive cycle devoted to foraging (as opposed to return travel time and surface recovery time).
de Leeuw 1997	tufted duck/pochard	travel time	strongly linearly correlated with water depth suggesting rates of travel approx constant
de Leeuw 1997	tufted duck/pochard	foraging time (on bottom)	highly positively correlated with water depth - spend longer on bottom in deeper water up to 6m. However, correlations were non-linear in both spp. Third order polynomials best fit in both cases i.e. bottom time levels off at greater depths with minor oscillations.
de Leeuw 1997	tufted duck/pochard	surface time	highly positively correlated with water depth - and significantly non-linear in both cases with a third order polynomial giving best fit initial increase then level off then another increase
de Leeuw 1997	tufted duck/pochard	foraging time (on bottom)	significant decline in the PROPORTION of dive cycle spent on bottom foraging with increasing water depth
de Leeuw 1997	tufted duck	foraging time (on bottom)	tufties significantly reduced the time spent foraging on bottom in response to increasing sand depth in which prey buried
de Leeuw 1997	tufted duck	surface time	surface time increased significantly in response to decreasing water temperature (except in the shallowest dives)
de Leeuw 1997	tufted duck	descent time	increased with diving depth (1.5m-5.5m)

de Leeuw 1997	tufted duck	foraging time (on bottom)	increased with diving depth (1.5m-5.5m)
de Leeuw 1997	tufted duck	surface time	increased with diving depth (1.5m-5.5m)
de Leeuw 1997	tufted duck	recovery time (mins)	increased with diving depth (1.5m-5.5m)
de Leeuw 1997	tufted duck	recovery time (mins)	increased with bout dive duration and its square term after backward deletion of depth and depth sq
de Leeuw 1997	tufted duck	recovery time (mins)	most diving ducks do indeed prefer to rest during the day time hours at sheltered areas. From an energetic point of view, resting periods thus seem to be of great importance in order to balance the energy budget (when cooled body temperatures can be recovered)
Draulans 1982	tufted duck	dive duration	significantly affected by both prey density (declines up to 944mussels/sq m and then increase again (due to increasing selectivity? Above 1000 per sq m) and diving depth (increased up to 4m depth and then levelled off)
Dunthorn 1971	common eider	dive duration (s)	the eiders collected the mussels during dives lasting from 6 to 60 seconds
Guillemette et al 1992	common eider	dive duration	crab feeding bouts also had the longest dive durations. This was expected as crabs were sparsely scattered on the bottom. Searching effort was probably an important part of diving time when feeding on crabs. In contrast, diving duration was the shortest when feeding on urchins. This was not surprising given that urchins were ubiquitous in the sub tidal zone (90 per sq m) .**Thus in these cases low prey density leads to longer bottom times as birds have to search for longer to find prey. However, the longer duration of dives for mussels compared to those for urchins was because a high number of prey was collected during each dive , whereas only a single urchin could be captured per dive.**
Guillemette 1998	common eider	dive:pause ratios	pause duration was 1.206, 1.240 and 1.163 times dive durations in mid winter, late winter and spring respectively. These values do not differ ie the dive to pause ratio is constant across time so no evidence that eiders compensate for less daylight hours in mid-winter by increasing the proportion of each dive cycle that is spent underwater as opposed to resting on the surface between bouts

Guillemette 1998	common eider	dive duration (s)	means of 22s, 26s and 22s in mid winter, late winter and spring when feeding in water depths of 0-3m
Guillemette 2001	common eider	dive:pause ratios	pause duration was 1.10, 1.11, 1.16 and 1.57 times dive durations in spring for females and males of two subspecies.
Guillemette et al 1992	common eider	dive duration	prey density also influences the duration of dive cycles. For example, when prey density is high, as when eiders feed in kelp beds and urchin barrens, dive duration is low compared to when eiders feed on the scattered crabs in the agarum beds. Similarly, Draulans 1982 and Tome 1988 demonstrate experimentally that diving duration in benthic diving ducks increases as prey density decreases - SEARCHING TIME REQUIRED
Guillemette et al 2004	common eider	foraging time (on bottom)	when averaged for each female, the data were qualitatively similar to theoretical predictions since travel, bottom and surface durations all increased with depth. However, within individual females the data supported the theory partially because some relationships between depth and phases of a dive cycle were not significant. In particular, bottom duration failed to increase with depth for two individual females during the summer.
Guillemette et al 2004	common eider	foraging time (on bottom)	Diving theory predicts that i) total diving time, ii) travel time iii) bottom time and iv) surface durations should increase with depth. That bottom duration should increase with depth but then decrease when depth increases beyond a certain value is a novel prediction from the theory of Houston & carbone (1992)
Guillemette et al 2004	common eider	foraging time (on bottom)	one prediction of the model by Houston & Carbone (1992) is that ducks will spend less time on the bottom if the energetic costs of foraging increase. In contrast to that prediction, Lalsey et al (2003) found that the duration of foraging on the bottom increased when diving costs were experimentally increased.
Guillemette et al 2004	common eider	foraging time (on bottom)	most of the time spent on the bottom by common eiders is devoted to the ingestion of prey as almost no mussel are swallowed at the surface (Guillemette 1998)
Guillemette et al 2004	common eider	dive duration (s)	presents 6 linear equations relating dive duration to water depth up to maximum depths of between 2.5m and 9m

Guillemette et al 2004	common eider	travel time	presents 6 linear equations relating travel time (s) to water depth up to maximum depths of between 2.5m and 9m
Guillemette et al 2004	common eider	foraging time (on bottom)	presents 6 linear equations relating foraging time on bottom (s) to water depth up to maximum depths of between 2.5m and 9m
Guillemette et al 2004	common eider	surface time	presents 6 linear equations relating surface time (s) to water depth up to maximum depths of between 2.5m and 9m
Guillemette et al 2004	common eider	dive duration (s)	in summer the dive duration was strongly and significantly correlated with depth for the 4 experimental females. However, the slope relating these two variables differed significantly BETWEEN females.
Guillemette et al 2004	common eider	travel time	in summer, travel duration was also highly and significantly correlated with depth for all females in summer. Again the slopes of these relationships differed between females.
Guillemette et al 2004	common eider	foraging time (on bottom)	in summer there was no significant correlation between water depth and bottom duration for two females in summer (the two with the shallowest max dive depth) whereas there were significant and positive correlations for the other two females
Guillemette et al 2004	common eider	surface time	in summer a weak but significant positive correlation between surface duration and depth was obtained for three females out of 4. Again there was considerable variation in the slope of this relationship between females.
Guillemette et al 2004	common eider	dive duration (s)	in winter dive duration was strongly and significantly correlated with depth for the 2 experimental females
Guillemette et al 2004	common eider	travel time	in winter travel time was strongly and significantly correlated with depth for the 2 experimental females
Guillemette et al 2004	common eider	foraging time (on bottom)	in winter bottom time was strongly and significantly correlated with depth for the 2 experimental females
Guillemette et al 2004	common eider	surface time	in winter surface time was strongly and significantly correlated with depth for the 2 experimental females
Guillemette et al 2004	common eider	all phases	interestingly, the slopes relating water depth with the duration of all phases of the diving cycle differed between seasons within individual females

Guillemette et al 2004	common eider	whole dive cycle (s)	the average duration of dive cycles in our study ranged from 32s to 98s
Guillemette et al 2004	common eider	all phases	the variation explained by water depth was less for surface duration (0-18%) than for bottom time (0-32%) and travel time (46-77%) . This is consistent with the findings of Kramer (1988) who found that the relationship between depth and surface e time between dives was variable and weak in a number of aquatic birds and mammals.
Guillemette et al 2004	common eider	travel time	the difference in the slope relating travel time to water depth between the females indicated that they were modulating speed at different rates while travelling.
Guillemette et al 2004	common eider	foraging time (on bottom)	blue mussel densities can vary considerably in space and time which MAY influence the duration spent on the bottom. However, Houston & Carbone's (1992) model predicted only a SLIGHT influence of patch quality on bottom duration
Guillemette et al 2004	common eider	foraging time (on bottom)	There was no evidence that bottom time of female common eiders first increased and then decreased the deeper the female dove (as was predicted by theory). The only exception was for female T in winter where the coefficient of determination of a quadratic function was marginally higher (rsq=0.076) than a linear function (rsq=0,056). Interestingly, the deepest dives achieved in our study were performed by this female. This lack of effect may be because the recorded depths in this study were quite low compared with eider's diving capability (up to 42m Guillemette et al 1993)
kramer 1988		dive duration	frequently increase with depth. The depth-time relationship in diving birds was noted by Dewar (1924)
kramer 1988		surface time	surface times also increase with diving depth in a number of species as predicted. Species in which surface times show a positive relationship to diving depth include many diving birds studied by Dewar 1924, cormorants and tufted ducks
Mori & Boyd 2004	fur seal	foraging time (on bottom)	time spent at the bottom of dives was used as an indicator of patch quality and was well correlated (p=0.045 n=5) with independent measures of prey abundance.
Nilsson 1972	scoters	dive:pause ratios	in shallow water

Parkes et al 2002	tufted duck	surface time	incorporating a biphasic oxygen uptake curve (walton et al 1998) means that due to the initial rapid resaturation of oxygen into the respiratory oxygen stores upon surfacing (due to more rapid breathing) a range of dive depths and associated travel times/times underwater will have identical surface times. According to the predictions of walton et al (1998) **a range of dives up to a certain duration will be associated with very similar surface durations** because the tangent from travel time will be locked to the kink in the cumulative oxygen stores with increasing surface time. This idea is in fact more or less consistent with the dive model used in the scoter model which, based on experimental observations that the rate at which surface times increase with increasing dive depth increases above a certain water depth, included a lower rate of surface time increase in shallow water ie when dives are short and a more rapid increase thereafter for deeper (longer) dives.
Parkes et al 2002	tufted duck	surface time	The biphasic nature of the oxygen uptake following longer (but not shorter dives) may be explained by a fairly sudden slowing (from an initial fast rate) of ventilation rate after the first three exhalations.
Reynolds 1987	long-tailed duck	dive duration	male dive times were significantly longer than those of females. This may be a consequence of physiological differences in diving ability. The latter has been shown to be very closely linked to body size in vertebrates.
Reynolds 1987	long-tailed duck	dive duration	Site related variations in the abundance and availability of potential prey items may also be of importance in determining dive durations
Stephenson et al 1986	tufted duck	dive duration (s)	linearly correlated with dive depth
Stephenson et al 1986	tufted duck	surface time	was not correlated with duration or with distance of the previous or following dive. Pause duration was very variable and appeared to depend very much on factors other than dive durations or feeding time on the bottom.
Stephenson et al 1986	tufted duck	dive duration (s)	mean 19.8 secs

Stephenson et al 1986	tufted duck	dive duration	during normal feeding dives the ducks probably remain fully aerobic and in this case feeding time on the bottom may be influenced by a number of other factors such as food density, particle selection time and handling time and or by the rate of food ingestion (as opposed to physiological factors such as changes in blood gas levels or acid-base disturbances that may be involved in terminating feeding in (artificially) extended dives)
Walton et al 1998	all diving birds	dive:surface ratio	the existence of a non-monotonic relationship between the dive to surface ratio and dive duration with the ratio peaking at a certain dive duration is a qualitative prediction of Kramer's (1988) and Houston & Carbone's (1992) models when avian physiology is incorporated ie a large % of the total air store being in the respiratory tract which can be replenished far faster than can the oxygen stored in the blood stream via gas exchange. However, this may not be the case when the blood oxygen stores are heavily depleted too (in which case the gain rate will be much higher during recovery than otherwise) which may occur when birds are constrained to spend a considerable time travelling to and from a relatively deep foraging area.
Walton et al 1998	all diving birds	dive:surface ratio	In this study, a peak in the dive to surface ratio / dive duration relationship was recorded in all three (Pursuit diving) species investigated. The peak in dive to surface ratio occurred only in short dives. Our hypothesis is that in certain situations, maximising time spent underwater (per dive cycle) is appropriate in birds (especially where a high proportion of the time underwater is devoted to searching)
Walton et al 1998	all diving birds	dive:surface ratio	Here, (ie cases in which the birds probably forage on the bottom) maximising the proportion of the dive cycle spent at the site of resource gain is more likely to approximate to maximising net rate of energy gain than is maximising the dive to surface ratio (Wilson & Wilson 1988, Houston & Carbone 1992).

Walton et al 1998	all diving birds	dive:surface ratio	In situations where dives can be relatively short, the unique respiratory physiology of birds allows then to adjust time allocation over the dive cycle so that surface time is minimised in relation to underwater time.
Wilson & Quintana 2004	imperial cormorant	dive:surface ratio	surface pauses increase according to a power function of time spent in the dive ie underwater or water depth.
Wilson & Quintana 2004	imperial cormorant	dive:surface ratio	the model predicted that imperial cormorants do not submerge with just enough oxygen to cover their projected dive performance but rather dive with a substantial reserve, although this reserve of oxygen decreases with increasing depth/duration.
Wilson & Quintana 2004	imperial cormorant	descent time	increases linearly with water depth (up to 70m) (rsq 90%)
Wilson & Quintana 2004	imperial cormorant	ascent time	increases linearly with water depth (up to 70m) (rsq 84%)
Wilson & Quintana 2004	imperial cormorant	foraging time (on bottom)	increases linearly with water depth (up to 70m) (r sq 38%)
Wilson & Quintana 2004	imperial cormorant	dive duration (s)	increases linearly with water depth (up to 70m) (rsq 77%)
Wilson & Quintana 2004	imperial cormorant	surface time	during deeper longer dives, the pauses on the surface became proportionally longer (power curve with a cubic term) (rsq = 65%)
Wilson & Quintana 2004	imperial cormorant	surface time	The major element in our model that affects the outcome is the form of the recovery duration/ dive duration regression. In a paper summarizing data from 19 cormorant species Cooper (1986) considered the relationship between inter dive interval and dive duration to be LINEAR, ALTHOUGH DEPTHS WERE GENERALLY SHALLOW AND DIVE DURATIONS SHORT. In contrast, both Croxall (1991) and Wanless (1993) note that long dive durations result in OVERLY long subsequent surface pauses. Kramer *(1988) postulated that recovery duration should increase as a power function of dive duration and this is ultimately close to that observed by us..

Wilson & Quintana 2004	imperial cormorant	surface time	Although accelerating surface pause durations with respect to dive durations are often used to invoke anaerobic metabolism (refs) this is not necessarily the case since the oxygen saturation curve over time is not linear, so that as diving animals use an increasing proportion of their overall oxygen stores (or have to attain higher and higher levels of pre-dive oxygen concentration for deeper and longer dives), recovery durations are expected to accelerate with respect to dive duration (Kramer 1988)
Ydenberg & Guillemette 1991	common eider	surface time	the length of each pause on the surface between dives increases at an increasing rate with the length of the preceding dive (and generates a humped dive:pause ratio v dive time).
Ydenberg & Guillemette 1991	common eider	surface time	we arbitrarily decided to exclude from the analysis, dive-pause cycles whose pause lasted MORE THAN 90s. This is conservative because the expected pause for the very longest dives of 72secs, is about 68 secs,
Ydenberg & Guillemette 1991	common eider	dive duration maximum observed (s)	72s
Ydenberg & Guillemette 1991	common eider	surface time maximum predicted at max observed dive duration (s)	68s
Ydenberg & Guillemette 1991	common eider	surface time as function of dive time	is very slightly but significantly concave up ie accelerating (pause(s)=11.24 + 0.46dive + 0.005divesq rsq=31.2%)
Ydenberg & Guillemette 1991	common eider	surface time as function of dive time	eiders alternate between periods when their pauses are shorter than expected given the preceding dive durations and periods when they are longer than expected but do so to a lesser degree than western grebes. The difference probably reflects the fact that the eiders feed on sessile prey whereas the grebes feed on mobile prey shoals that may escape - necessitating intense activity for short periods from which they recover later.

Ydenberg & Guillemette 1991	common eider	surface time as function of dive time	IS ACCELERATED IN EIDERS BUT NOT IN WESTERN GREBES. YDENBERG (1988) HAS PREVIOUSLY NOTED THESE DIFFERENCES BETWEEN DIVING DUCKS AND OTHER DIVERS SUCH AS GREBES.

Appendix 3 Notes concerning the speed of swimming while underwater

source	species	parameter	ascent/ descent	min	value	max	comments
Beauchamp et al 1992	common eider	descent speeds					assumed here that the speed at which an eider travels to and from the bottom is constant
Beauchamp et al 1992	cormorant	descent speeds					travel speed at the bottom increases with depth ie birds descend faster the deeper they go
Carbone & Houston 1994	pochard	diving speed					durations of descent and ascent were linearly related with depth suggesting that both stages of travel were at a constant speed
Carbone & Houston 1994	pochard	diving speed (m/sec)	both		0.476		at depth of 0.5m, this is the average of ascent and descent speeds
Carbone & Houston 1994	pochard	diving speed (m/sec)	both		0.79		at depth of 3.0m, this is the average of ascent and descent speeds
Carbone & Houston 1994	pochard	travel time					increased significantly with depth
Carbone 1995	pochard	travel speed	both		0.88		travel time increases linearly with water depth, suggesting that travel speeds are constant. This constancy appears to be a reasonable assumption under most conditions. Observed changes in travel speed are small and probably only cause slight error in the estimates of travel time.
Carbone et al 1996	tufted duck/pochard	travel speed average over up and down (m/sec)	both		1.31		changes in return travel time with depth were strongly linear suggesting that rates of travel were approx constant.
Carbone et al 1996	tufted duck/pochard	ascent duration					birds ascend more rapidly when the water is colder.
Carbone et al 1996	tufted duck/pochard	ascent duration					birds ascend more rapidly when the water is colder.
Carbone et al 1996	tufted duck/pochard	descent speeds					significantly faster at the surface near the start of a dive then deeper later in a dive.

Carbone et al 1996	tufted duck/pochard	ascent speeds					significantly faster at the surface near the end of a dive then deeper earlier in the ascent.
Carbone et al 1996	tufted duck/pochard	ascent speeds					significantly faster at the surface near the end of a dive then deeper earlier in the ascent.
de Leeuw 1997	tufted duck	swimming speed (vertical descent) (m/s)	descent		0.748		upper part of dive in 3.3m of water
de Leeuw 1997	tufted duck	swimming speed (vertical descent) (m/s)	descent		0.69		lower part of dive in 3.3m of water
de Leeuw 1997	tufted duck	swimming speed (vertical descent) (m/s)	descent		0.782		upper part of dive in 5.5m of water
de Leeuw 1997	tufted duck	swimming speed (vertical descent) (m/s)	descent		0.694		lower part of dive in 5.5m of water
de Leeuw 1997	tufted duck	swimming speed (vertical ascent) (m/s)	ascent		1.67		upper part of dive in 3.3m of water
de Leeuw 1997	tufted duck	swimming speed (vertical ascent) (m/s)	ascent		0.822		lower part of dive in 3.3m of water
de Leeuw 1997	tufted duck	swimming speed (vertical ascent) (m/s)	ascent		1.16		upper part of dive in 5.5m of water
de Leeuw 1997	tufted duck	swimming speed (vertical ascent) (m/s)	ascent		0.94		lower part of dive in 5.5m of water
de Leeuw 1997	tufted duck/pochard	travel time (to and from bottom)					strongly linearly correlated with water depth suggesting rates of travel approx constant
de Leeuw 1997	tufted duck	descent time					increased with diving depth (1.5m-5.5m)
de Leeuw 1997	tufted duck	ascent time					increased with diving depth (1.5m-5.5m)

de Leeuw 1997	tufted duck	ascent time					increased with diving depth (1.5m-5.5m)
de Leeuw 1997	tufted duck	speed of descent (m/sec)	descent		0.66		did not vary between depths
de Leeuw 1997	tufted duck	diving speeds (ascent) m/s	ascent	0.65		1	increased with water depth
Guillemette 1998	common eider	speed of descent (m/sec)	descent		0.952		
Guillemette 1998	common eider	swimming speed of descent (m/sec)	descent		0.952		
Guillemette et al 2004	common eider	diving speed (average of up and down) (m/sec)		0.264	0.332	0.478	based on 12 values derived from 6 regression equations at depths of 1m and 3m combined. We speculate that this variation in travel speeds is induced by seasonal variation in body mass as it fluctuates drastically during the annual cycle. Body mass changes substantially affect buoyancy in birds.
Hawkins et al 2000	common eider	swimming speed				1.3	no bird was able to swim against current speeds of more than 1.3m/sec
Hawkins et al 2000	common eider	descent method					beating still partly folded wings AND stroking with the feet which beat simultaneously.
Hawkins et al 2000	common eider	ascent method					entirely passive- the duck stopped beating her wings and feet and floated to the surface.
Hawkins et al 2000	common eider	ascent method					entirely passive- the duck stopped beating her wings and feet and floated to the surface.
Lovvorn & Jones 1991	lesser scaup	diving speed (m/sec) (descent)	descent		0.67		
Lovvorn & Jones 1991	lesser scaup	diving speed (m/sec) (ascent)	ascent		0.69		
Lovvorn et al 1991	canvasback	speed of descent (m/sec)	descent		0.93		
Lovvorn et al 1991	redhead	speed of descent (m/sec)	descent		0.91		

Lovvorn et al 1991	lesser scaup	speed of descent (m/sec)	descent		0.68		
Lovvorn et al 1991	canvasback	swimming speed of descent (m/sec)	descent		0.93		
Lovvorn et al 1991	lesser scaup	swimming speed of descent (m/sec)	descent		0.68		
Lovvorn et al 1991	redhead	swimming speed of descent (m/sec)	descent		0.91		
Stephenson 1994	lesser scaup	travel speed	descent		0.63		in descent
Stephenson et al 1986	tufted duck	swimming speed (vertical descent) (m/s)	descent		0.57		
Stephenson et al 1986	tufted duck	swimming speed (vertical ascent) (m/s)	ascent		0.61		
Wilson & Quintana 2004	imperial cormorant	speed of descent (m/sec)	descent		0.67		constant with respect to depth
Wilson & Quintana 2004	imperial cormorant	diving speeds (ascent) m/s	ascent		0.67		constant with respect to depth

Appendix 4 Notes concerning the daytime and night time feeding activity of diving ducks

source	species	season	parameter	value	comments
Bustnes & Lonne 1997	common eider	winter	day/night	day	eiders are mostly diurnal feeders (6 refs) and probably depend much on VISION to locate food in areas where the prey are dispersed
Campbell 1978	common eider	winter	day/ night/ tidal		in the Ythan and Tay the TIDE was considered to be the dominant factor driving eider feeding patterns whereas in Norway and west Scotland DIURNAL routines were more evident. (various refs)
Campbell 1978	common eider	winter	day/ night/ tidal		Player (1971) suggested that the feeding flock at Leith was influenced by both factors
Campbell 1978	common eider	winter	day/night	DAY	eiders flighted into the area at dawn and moved away again during the course of the day towards dusk. The first birds arrived 25-30mins before sunrise, the majority being present by then
Campbell 1978	common eider	winter	day/ night/ tidal		the size of the dawn influx was dependent on the state of the tide at dawn though being highest when sunrise coincided with the last stages of an ebbing tide and lowest on a flooding tide.
Campbell 1978	common eider	winter	day/night	DAY	the eiders moved east at dusk
Campbell 1978	common eider	winter	day/night	DAY	movements of large numbers offshore at dusk and inshore again at dawn were detected on 6 occasions at Musselburgh. Some were estimated to have flown at least 4km offshore before disappearing from sight.
Campbell 1978	common eider	winter	day/night	DAY	The main pattern of behaviour was a DIURNAL one, eiders moving at dawn and dusk between separate areas used by day and at night. The dusk peak activity in foraging and the dawn element of attraction of birds to Leith were indications that the eiders DID NOT FEED AT NIGHT
Cramp & Simmons 1977	common scoter		day/night	day	mainly a daytime feeder often in closely grouped flocks with regular massed dives
Cramp & Simmons 1977	common scoter		day/night	day	mainly diurnal feeder so roosts nocturnally as well as loafing periodically during day

Cramp & Simmons 1977	velvet scoter		day/night	day	normally daytime feeder, often gregarious with synchronised diving
Cramp & Simmons 1977	velvet scoter	all year	day/night	day	at all times, essentially diurnal feeder, roosting nocturnally with periods of loafing during day.
de Leeuw 1997	diving ducks		day/night	night	in the wild, diving ducks usually feed at night and rest during the day.
Draulans 1987	pochard		day/night	night	nocturnal tactile feeders
Draulans 1987	tufted duck		day/night	night	nocturnal tactile feeders
Dunthorn 1971	common eider		day/night	day?	the birds came to the mussel ropes about two hours after first light
Dunthorn 1971	common eider		day/night		in the evening they went to the south. Here they took other food organisms (Carcinus, Littorina and echinoderms)
Durinck et al 1993	common scoter		day/night	night?	birds caught in bottom set nets laid out overnight
Goudie & Ankney 1986	common scoter		day/night	day	
Guillemette 1998	common eider		day/night	day BUT	although some authors have stated that eiders and sea ducks in general are diurnal birds, NONE HAS PRESENTED EVIDENCE TO SUPPORT THIS
Guillemette 1998	common eider	winter	day/night	day	THUS IT MAY BE CONSIDERED THAT COMMON EIDERS IN WINTER FORAGE MOSTLY DURING THE DAY AND THAT NIGHT FORAGING IF ANY IS RARE.
Guillemette 1998	common eider		day night		night feeding is related to the digestion constraint and ingestion of a large bulk of shell material associated with eating large molluscs
Guillemette 1998	common eider	winter	day/night	day	this study is based on the main assumption that eiders are DIURNAL. Although some authors have stated that eider and seaducks in general are diurnal birds (Nilsson 1972, Stott & Olson 1973, Goudie & Ankney 1986) but none has presented evidence to support this.

Guillemette 1998	common eider	winter	day/night	day	two lines of evidence support the assumption that they are diurnal. First, no birds were seen foraging later than half an hour after sunset since they had stopped diving and were leaving the study site swimming offshore.. On only one occasion were eiders seen foraging over a reef during the full moon suggesting that common eiders are at least able to forage in dim light.
Guillemette 1998	common eider	winter	day/night	day	Secondly, no birds were seen at the study site before dawn. Eiders only were seen flying in from offshore locations and typically started to land at the study site around sunrise.
Guillemette 1998	common eider	winter	day/night	facultative night feeder	Interestingly, Nehls (pc) observed that common eider in the Wadden sea were active a small proportion of the night, feeding in the intertidal and subtidal zone. In contrast, Systad (1995) observed that common eiders wintering in northern Norway do not feed during the night while studies from that area (Bustnes & Erikstad 1990) showed that the size of mussels ingested there was small (median = 13mm) (cf c 42mm in Wadden Sea). From this I suggest that common eider are NON-OBLIGATORY DIURNAL FEEDERS and that night feeding is related to the digestion constraint and ingestion of a large bulk of shell material associated with eating large molluscs.
Kirby et al 1993	velvet scoter	winter	day/night	day	
Leopold 2002	common eider	winter	day/night	day	when the boat was moved again in the falling darkness, few birds followed. A bright lamp was lit at the stern and 10 birds foraged for another 15mins in the lamplight close to the stern, but disappeared soon after. Again, this was their normal behaviour.
Lewis et al 2005	Aythyini		day/night	night	Some non-sea duck species of diving ducks (tribe Aythyini) commonly prey upon bivalves at night (refs). Therefore, scoters could potentially utilise nocturnal foraging.
Lewis et al 2005	harlequin duck	winter	day/night	day	harlequin ducks at 60 degrees N did NOT forage at night (source Rizzolo et al 2005)

Lewis et al 2005	sea ducks		day/night	day	most sea duck species (tribe Mergini) are thought to be diurnal foragers (refs) although few data exist to adequately address this ASSUMPTION. This information gap limits thorough understanding of sea duck foraging ecology and energetics
Lewis et al 2005	sea ducks		day/night	both	recent data from high latitudes (70degrees) have demonstrated nocturnal feeding by some sea duck species during the shortest days of winter (Systad & Bustnes 2001). These nocturnal foragers fed in shallow water and employed non-diving feeding behaviours such as surface feeding and up-ending
Lewis et al 2005	sea ducks		day/night	both	Nocturnal foraging studies of other sea duck species have been conducted at HIGH LATITUDES.
Lewis et al 2005	stellers eider	winter	day/night	both	Systad & Bustnes (2001) documented nocturnal foraging and increased crepuscular foraging activity by Stellers eiders during the shortest days of winter at 70 degrees N
Lewis et al 2005	surf and white-winged scoters		day/night	day	are believed to feed only diurnally (McNeil et al 1992), although no studies have attempted to directly measure their nocturnal foraging during winter
Lewis et al 2005	surf and white-winged scoters		day/night	day (virtually exclusively)	98% of diurnal time periods contained diving activity compared to only 2% of nocturnal time periods. Results were very similar for both species
Lewis et al 2005	surf and white-winged scoters		day/night	day (virtually exclusively)	in general, both scoter species were located within intertidal areas during diurnal hours and in subtidal ie over deeper areas during nocturnal hours. At night they were also further from the shore. These observations indicate that the birds WERE NOT utilising alternative non-diving feeding techniques in shallow water at night.
Lewis et al 2005	surf and white-winged scoters		day/night	day (virtually exclusively)	Our results indicated that Surf scoters and white-winged scoters RARELY FORAGE AT NIGHT

Lewis et al 2005	surf and white-winged scoters		day/night	both	THE FACT THAT WE OBSERVED NOCTURNAL FORAGING ALBEIT RARELY SUGGESTS THAT SCOTERS POSSESS THIS ABILITY (maybe the very little diving recorded at night in deep water was NOT foraging though???). It appears however that in general at this study site 50 degrees N, scoters are CHOOSING not to forage nocturnally. Non profitable foraging (due to lack of visual cues, nocturnal predation risk (in inshore feeding grounds) and visual constraints acting solely or in combination could potentially force scoters to avoid nocturnal foraging. Also, acquisition of sufficient energy during daylight may pre-empt the need for nocturnal foraging.
Marsden 2000	tufted duck/pochard	winter	day/night	both	generally, more feeding occurred at night. Daytime feeding levels were significantly higher on days that were colder than the previous day had been
Mudge & Allen 1980	common eider/ common scoter	winter	day/night	day	the behaviour of sea duck flocks at dusk suggested that most species spent the night away from the daytime feeding areas. Eiders, common scoters and velvet scoters swam offshore at dusk and probably spent the night on the sea close by.
Nehls 1995	common eider		day/night	both	two out of three birds dived virtually only during daylight on four days in mid-winter. One bird did dive during darkness on all four days.Fig 7.11
Nehls 1995	common eider		day/night	both	Fig 7.12 shows that between January and March the bulk of diving is done during daylight hours (especially towards the end of the day) but that some lower-level of diving does occur at night. Night diving is more common in January and becomes less frequent in February and virtually non-existent in March.
Nehls 1995	common eider	spring and early summer	day/night	day only	eiders preferred to feed in daylight and were exclusively diurnal foragers in spring and early summer.
Nehls 1995	common eider	winter	day/night	both	In winter eiders foraged both at day and at night
Nehls 1995	common eider	moult period	day/night	night	in the moult period eiders foraged for a few weeks mainly at night

Pedroli 1982	tufted duck	winter	day/night	night	during the night the birds have their diving activity. Between 30% and 50% of the night time was devoted to diving (cf daytime when feeding occurred only seldom
Pedroli 1982		winter	day/night	night	Nilsson (1970 thesis) in Sweden concluded that tufties, pochard and greater scaup had a nocturnal feeding activity.
Pedroli 1982		winter	day/night	night	most species of diving ducks feed during the night and rest during the day. In the great number of cases nocturnal feeding was attributed to human disturbance on feeding grounds during the day, mostly near the shore
Raffaelli et al 1990	common eider		day/night	both	eiders feed on each low tide, EVEN AT NIGHT, with individual birds feeding for about 4 hours each 24 hour period (H Milne pers comm)
Rizzolo et al 2005	harlequin duck	winter	day/night	day only	At 60 degrees North, we found no evidence of nocturnal dive feeding (by radio tracking). Signals from 8 tagged birds never exhibited signal loss due to diving at night. In contrast, the same 8 birds exhibited signal loss during 62% +/- 7% (se) of 365 * 5 minute foraging periods during daylight.
Rizzolo et al 2005	harlequin duck	winter	day/night	day only	Harlequin ducks rest in groups offshore at night (refs). Low signal strength at night suggested that the birds were not near shore and we also observed daily offshore movements shortly after sunset by harlequin ducks, as have been documented at other wintering sites (refs). This hypothesis is supported by increased foraging rates during the evening by wintering harlequin ducks that suggests preparation for a period of non-feeding during the night (refs)
Rizzolo et al 2005	king and common eiders	winter	day/night	both	King eiders and common eiders responded to reduced photoperiod and harsh weather conditions at a 70 degrees N latitude wintering site by foraging during early morning and late evening darkness suggesting that these species were able to forage profitably under low light conditions (perhaps because of reliance on primarily sessile prey) (source Systad et al 2000)

Rizzolo et al 2005	stellers eider	winter	day/night	both	Sysad & Bustnes (2001) found that stellers eiders wintering at 70 degrees N forage at night during midwinter and likely decreased the foraging costs by increasing their use of NON_DIVING foraging behaviours (surface feeding , upending) and concentrating foraging activity during low tide
Rodway & Cooke 2001	harlequin duck	winter-spring	day/night	day only	harlequin ducks (at 49 degrees N) avoid crepuscular and nocturnal periods near shore when not constrained by food availability and the length of daylight in which to feed
Rodway & Cooke 2001	harlequin duck	winter-spring	day/night	day only	Harlequin ducks forage diurnally and move to offshore waters at night. During winter they spend the majority of daylight hours feeding (Goudie & Ankney 1986).
Rodway & Cooke 2001	harlequin duck	winter-spring	day/night	day only	Harlequin ducks were never seen near shore during the night. Around sunset, birds in small flocks flew or swam 1-3km offshore where they spent the night.
Rodway & Cooke 2001	harlequin duck	winter-spring	day/night	day only	The earliest recorded arrival time was 32min before sunrise and latest departure was 32 mins after sunset both in Nov/Dec ie mid-winter. Offshore birds were not observed feeding during dawn or dusk but were observed preening
Rodway & Cooke 2001	harlequin duck	winter-spring	day/night	day only	there was no evidence of nocturnal foraging, although some individuals in winter fed near the shore until almost half an hour after sunset when it was getting quite dark (desperate individuals??). It is not clear why some diurnally foraging species with diets similar to some nocturnal feeders do not also feed nocturnally (Nilsson 1970)
Rodway & Cooke 2001	harlequin duck	winter-spring	day/night	both?	overall, harlequin ducks adjusted their activity patterns to avoid crepuscular and nocturnal periods near shore unless constrained by food availability and the length of daylight.. Some nocturnal feeding observed in other seaducks, and suspected in harlequin ducks elsewhere (Bengston 1966) suggests that harlequin ducks MAY BE CAPABLE OF FEEDING AFTER DARK.
Swennen 1976	common eider		day/night	both	in some cases the birds were observed to feed during the night

Swennen 1976	common eider		day/night	both	feeding of birds in captivity indicated that the start of daily feeding occurred about half an hour before sunrise in January and about half an hour after sunrise in June. The end of feeding was much more irregular than the beginning. Often animals went on feeding till long after sunset and sometimes they stopped in the afternoon only to feed again during some hours in the night
Swennen 1976	common eider		day/night	both	After a good deal of nightly feeding activity there used to be longer resting periods during the day. In winter, the part played by nocturnal activity was greater than in summer with the result that the average feeding time per 24h is more or less the same.
Systad & Bustnes 2001	common eider		day/night	DAY	NO NIGHT FEEDING AMONG COMMON EIDERS
Systad & Bustnes 2001	sea ducks		day/night	mainly diurnal	night feeding is thought to be rare amongst sea ducks ALTHOUGH THE EVIDENCE IS POOR
Systad & Bustnes 2001	stellers eider		day/night	mostly day	most likely to feed during daylight and twilight, but they also fed during darkness
Systad et al 2000	sea ducks		day/night	diurnal	

Appendix 5 Notes concerning the depletion of resources by diving ducks

source	species	Parameter	min	value	max	comments
Approp Assess 2005	common eider	depletion				losses of 90% of 1,600 tonnes of mussels noted from one bed ie the Roger (Trap) lay. A further 6,000 tonnes are at risk. But, other lay holders on Scotsman's sled had not noticed significant loss of mussels as yet and there have been NO REPORTS of significant predation by eider on the wild mussel beds. At present eider predation on mussels seems largely confined to lays on the Roger/Toft
Approp Assess 2005	common eider	depletion				given more realistic food requirements and population level variation over time, likely that eiders account for less than half of the observed mussel losses from the Roger Lay.
Brager et al 1995		depletion				whereas stocks of epibenthic molluscs may be destroyed completely or reduced below a profitable level in offshore shallow waters during winter , in coastal shallow waters their biomass usually decreases by only a small proportion over the winter (source Kirchhoff 1979)
Camphuysen et al 2002	common eider	available resources				in the year in which there was massive eider mortality in the Wadden Sea (1999-2000) the estimated total stock of shellfish flesh was 4.7 times the total requirement of the eider population. NB this calculation is very dodgy as it makes no assumptions about availability etc etc. In fact only 8.5% of the total resource was potentially suitable food in favoured, constantly accessible feeding areas. This equates to only 40% of the actual population requirements.

Cantin et al 1974	common eider	depletion	10%		30%	between 10 and 30% of the standing crop biomass of Littorina alone is removed by the ducklings and the females accompanying them.
Cantin et al 1974	common eider	depletion (% of stock removed)		15%		Littorina in Russia
Cantin et al 1974	common eider	depletion (% of stock removed)		2.70 %		Mytilus in Russia
Cantin et al 1974	common eider	depletion (% of stock removed)				in depths less than 30m, common eider predation was sufficient to balance the annual production of Chlamys islandica
Cantin et al 1974	common eider	depletion (% of stock removed)		30%		all of the annual production by Mytilus edulis in the Ythan may be accounted for in terms of predation, of which eiders represented 30%
de leeuw 1997	tufted duck/pochard	giving up densities				at the end of the predation period were inversely related to supposed costs for exploitation (water depth)
de leeuw 1997	tufted duck/pochard	giving up densities				were weakly related to initial mussel biomass but strongly related to the average biomass available in the surrounding environment. In the rich environment, significantly more mussels were left than in the poor environment.
de leeuw 1997	tufted duck/pochard	giving up densities				tends to be greater at greater depths because less rewarding (flight from coastal roost sites to deep water, diving to greater depth, lower flesh content of mussels)
de leeuw 1997	tufted duck/pochard	depletion	10%	18%	44%	of the food stock is consumed each winter
de leeuw 1997	diving ducks	depletion	5%		35%	on Mytilus
de leeuw 1997	common eider	depletion		13%		mussels and cockles
de leeuw 1997	common eider	depletion	48%		69%	Mytilus
de leeuw 1997	diving ducks	depletion		22%		Dreissena
de leeuw 1997	diving ducks	depletion		57%		Dreissena
de leeuw 1997	diving ducks	depletion		95%		Dreissena

de leeuw 1997	scaup	GIVING UP DENSITIES (gFW per sq m)		30		other values given for scaup are 47 and 60
de leeuw 1997	tufted ducks/scaup	GIVING UP DENSITIES (gFW per sq m)	30		100	GUD increases with water depth because intake rates are lower at greater depth
de leeuw 1997	tufted ducks/scaup	depletion				depletion of the profitable shallow areas will reduce intake rate when mussel densities become low, thereby increasing the foraging costs to maintain energy balance. Eventually it will pay the ducks to shift to deeper water.
de leeuw 1997	diving ducks	GIVING UP DENSITIES (gFW per sq m)		50		the average giving up density in a heterogeneous area will be higher than the threshold of a fully exploited patch. Here I provisionally accept a general GUD of 50gfw/sqm
de leeuw 1997		GIVING UP DENSITIES (gFW per sq m)				to approximate the effect of coarse level patchiness on habitat suitability the probability of encountering mussels was estimated from lake-wide surveys of mussels. Grid cells of 2x2km with average densities of more than 50gFW/sqm were accepted as a functional feeding unit which can sustain a flock of ducks for several days.
de leeuw 1997	diving ducks	GIVING UP DENSITIES (gFW per sq m)				as a relative estimate for the probability of finding mussels in a grid cell I will use the percentage of bottom samples in which mussels were found.
Draulans 1982	tufted duck	depletion				predation was most intense in the areas with the highest prey densities. The increase in predation rate with increasing mussel density was highly significant
Draulans 1982	tufted duck	depletion				mussel density decreased as a consequence of duck predation at all five depths. Predation was however significantly higher at the shallowest depth.
Draulans 1982	tufted duck	depletion				birds feed more where mussel densities are high and the water is shallow. Depletion is greater in such places
Guillemette & Himmelman (1996)	common eider	depletion (of available biomass)		48-69%		estimated by Guillemette et al 1996 for mussel feeding eiders
Guillemette & Larsen	common eider	depletion	40%		70%	eiders may deplete their food substantially (40-70%) during the winter and may track food over large spatial and temporal scales (refs)

2002						
Guillemette & Larsen 2002	common eider	depletion	11%		37%	this suggests that other predators and other factors played a role in the disappearance of Cardium and Spisula during the winter
Guillemette & Larsen 2002	common eider	depletion				prey depletion drives the seasonal distribution of eiders (refs)
Guillemette 1998	common eider	depletion	40%		60%	eiders removed 40%-60% of the biomass in the course of the winter
Guillemette 1998	common eider	depletion (of available biomass)		40-60%		estimated by Guillemette et al 1996 for mussel feeding eiders
Guillemette et al 1996	common eider	depletion	21%	45%	69%	of the autumn biomass is removed when feeding on mussels. Eiders substantially deplete mussel beds in winter which in turn seems to affect their distribution
Guillemette et al 1996	common eider	depletion	3%		6%	of the autumn biomass is removed when feeding on sea urchins
Guillemette et al 1996	seaducks	depletion		6%		of the biomass of Mytilus edulis is consumed annually by the entire sea duck community in the Baltic
Guillemette et al 1996	common eider	depletion		12.5 %		of the biomass of Mytilus edulis and Cerastoderma present is consumed annually by eider ducks
Hamilton 2000	common eider	depletion				eiders fed heavily on blue mussels, reducing their abundance in exposed plots vs enclosures by nearly 50% within eight months of initiation of the experiment
Hart & Brown 2006	common eider	depletion				the numbers of eiders observed on the Roger lay during HW and the number observed foraging on or adjacent to the lay during LW declined in reflection of the loss of mussel beds after dredging. Many eiders may have exploited food resources outside the study area post fishing depletion. EG 1050 eiders and 1200 common scoters counted on Scull Ridge where dredge samples revealed an abundance of juvenile razor shells Ensis spp (ESFJC unpub data)

Hilgerloh 1997	common eider	depletion				predation (by eiders/ oysterctachers and herring gulls) could be compensated by 12% of production in 1991 and by 29% in 1994. Predation was responsible for 7% of the total elimination in 1991 and for 15% in 1994. Thus, factors other than predation by birds were responsible for 85-93% of elimination of mussel biomass
Hilgerloh 1997	VARIOUS SHELLFISH EATING BIRDS	depletion				Apparently stable mussel populations sustain a high yield to birds which can amount to about 70% of the total mussel production of an area or even 95% on a single mussel bed WITHOUT DESTABILISING THE MUSSEL POPULATION. THERE IS A TABLE 7 WITH FIGURES FOR PUBLISHED BIRD PREDATION RATES AS % OF PRODUCTION OR BIOMASS WHICH VARY ENORMOUSLY
Hilgerloh 1997	VARIOUS SHELLFISH EATING BIRDS	depletion				In an area of decreasing mussel stocks, predation is an elimination factor of minor importance, while on stable mussel beds predation accounts for a high proportion of the loss (but without necessarily destabilising the population - see previous note)
Larsen & Guillemette 2000	common eider	depletion		25 - 58%		of the energy available from blue mussels in the 0-6m depth range was consumed by eiders
Larsen & Guillemette 2000	common eider	depletion		1-3%		in the 6-12m depth range common eiders in both study areas exploited only a negligible part of the food biomass (deep water more costly and dominated by large unprofitable mussels as opposed to small ones in shallow water.)
Lovvorn & Gillingham 1996	canvasbacks	giving up densities				model canvasbacks could not forage profitably at the late winter time even although 26% of foraging loci available were still profitable. In other words not all the food is exploitable.
Lovvorn 1989	canvasbacks	depletion				sequential use of tubers and then clams appears to result from initially high foraging efficiency for tubers which declines as tubers are depleted
Lovvorn 1989	canvasbacks	depletion				clam populations (Macoma) fluctuate widely among years and different areas. Thus, effects of the loss of plant tubers (the preferred food) on canvasback populations probably depends on the frequency and extent of shortages of ALTERNATIVE clam foods

Lovvorn 1989	canvasbacks	depletion				Along two of four transects numbers and biomass of Vallisneria tubers declined substantially over the waterfowl staging period. On one other transect, and at deeper sediment layers on another, numbers and biomass of tubers increased indicating the plants were still growing after initial sampling. Thus, losses not due to die back but due to consumption by ducks especially of near surface tubers.
Lovvorn 1989	canvasbacks	depletion				depletion of tubers results in a shift to a clam diet in December
Lovvorn 1989	canvasbacks	depletion				intake rate for tubers is probably greater than for clams when canvasbacks arrive in autumn, This is probably influenced by the much lower mass-ingestion requirements of tubers than clams for producing body fat (higher assimilable energy per gram ingested???)
Lovvorn 1989	canvasbacks	depletion				The effects of the loss of tubers on canvasbaks at the population level depend primarily upon the frequency and extent of shortages of clams throughout the region. Thus, the highly publicised concern over submerged aquatic plants in this area should be extended in efforts to monitor and understand variations in clam abundance.
Mori & Boyd 2004	fur seal	depletion				we found that the index of patch quality declined during a bout, suggesting that there was a resource depletion during foraging.
Nehls & Ketzenberg 2002	common eider	depletion		20%		on mussels
Nehls & Ketzenberg 2002	common eider	depletion		80%		depletion to an extent where a resource is no longer exploitable is a common feature and has been noted for…and eiders which may remove more than 80% of their food stocks in areas where densities are high.
Nehls & Ketzenberg 2002	common eider	depletion		12%		consumption by eiders only reaches 12% of the average production of their prey spp ie mussels and cockles in the Wadden sea

Nehls & Ketzenberg 2002	common eider	depletion		40%		of the annual mussel production
Nehls & Ketzenberg 2002	common eider	depletion		55%		on mussel beds
Nehls & Ruth 1994	common eider	depletion				…production of the mussels compensates losses from eider predation
Nehls & Ruth 1994	common eider	depletion				as density-dependent growth appears to be an important factor in mussel culturing, it is likely that these losses are easily compensated by improved growth conditions of the remaining mussels. A similar situation was found on a natural intertidal bed where predation by eiders reduced mussel density but did NOT affect total biomass of the mussel bed (Nehls & ketzenberg)
Nehls & Ruth 1994	common eider	depletion		10-20%		of the annual production of their prey in the Wadden Sea (refs)
Nehls & Ruth 1994	common eider	depletion				…but from the available data it appears to be rather unlikely that this extensive use of mussel cultures in the Wadden Sea of SH may lead to measurable reductions of the fisheries yield.
Nehls 1989	common eider	depletion		5%		of the total biomass of the macrozoobenthos in Nordstrander Bay or the tidal flats of the Dutch Wadden Sea
Nehls 1989	common eider	depletion		12.5 %		of the total biomass for each of the two main prey species ie mussels and cockles
Nehls 1989	common eider	depletion		39%		of the annual mussel production is consumed by eiders on the Ythan (ie 20% of all zoobenthos production) (Milne & Dunnett 1972).
Nehls 1989	common eider	depletion		10-30%		In the St Lawrence estuary, Canada, eiders take during the summer 10-30% of their preferred prey, a Littorina spp (Cantin et al 1974)
Nilsson 1972	diving ducks	depletion		5%		the total food intake of all the diving ducks was about 5% of the observed decrease in standing crop between Nov and April
Nilsson 1972	diving ducks	depletion				The highest rates of exploitation occurred in the richest areas
Nilsson 1972	diving ducks	depletion				In all areas the calculated exploitation (depletion) was small in relation to the standing crop of potential food species

Raffaelli et al 1990	common eider	depletion		4360 mussels per sq m		removed by eiders from the mussel beds over a 60 day period. This loss was not across all mussel size classes, being greater proportionately among mussels of 10-25mm
Raffaelli et al 1990	common eider	depletion		36%		of the larger mussels (6-30mm) were removed over a 60 day experimental period
Raffaelli et al 1990	common eider	depletion		80%		a previous survey by Galbraith (unpub) indicated that 80% of mussels WITHIN THIS SIZE RANGE (6-30MM) DISAPPEAR FROM THE YTHAN BEDS BETWEEN NOV AND APRIL AND WHICH ARE ASSUMED TO BE MAINLY EATEN BY EIDERS
Scheiffarth & Nehls 1997	common eider	depletion (gAFDW per sq m per year)		1.26		this is the value for eiders alone for whole Sylt_Romo area (derived from the overall figure for all species and the 37% contribution of eider to this total)
Scheiffarth & Nehls 1997	common eider	depletion (gAFDW per sq m per year)		3.22		this is the value for eiders alone for intertidal parts of the Sylt_Romo area (derived from the overall figure for all species and the 37% contribution of eider to this total)
Scheiffarth & Nehls 1997	common eider	depletion (gAFDW per sq m per year)		11.52		this is the value for eiders alone for whole Konigshafen bay (derived from the overall figure for all species and the 60% contribution of eider to this total)
Scheiffarth & Nehls 1997	common eider	depletion (gAFDW per sq m per year)		10.56		this is the value for eiders alone for intertidal parts of the Konigshafen Bay (derived from the overall figure for all species and the 60% contribution of eider to this total)
Sekiya et al 2000	tufted duck	depletion		yes		after the mussel biomass decrease in late winter, tufties switched their diet to manila clams and Crustacea
Sekiya et al 2000	pochard	depletion		yes		after the mussel biomass decrease in late winter, pochard switched their diet to manila clams only
Sekiya et al 2000	tufted duck/pochard	depletion		yes		large mussels are exhausted by duck predation

Stott & Olson 1973	scoters	depletion		yes		Glude 1967 found that an increase in the number of scoters in a coastal shellfish area of Washington caused a reduction in numbers of commercial soft shelled clams.
Stott & Olson 1973	scoters	depletion		no		superficially it appeared that the food resource had not been severely depleted by the scoter population

Appendix 6 Notes concerning the diving depths of diving ducks

source	species	parameter	min (m)	value (m)	max (m)	comments
Approp Assess 2005	common eider	water depth	0.15		40	min from Player 1970 and max from Ross & Furness 2000
Brager et al 1995	common scoter	water depth			10	in this wintering area seaducks prefer shallow waters (<10m deep) for feeding
Brager et al 1995	common eider	water depth	5	8.4	9	immature eider
Brager et al 1995	common eider	water depth	9	11.2	20	adult eider
Bustnes & Lonne 1997	common eider	water depth			10	the common eider selected water shallower than 10m
Bustnes & Lonne 1997	king eider	water depth			>20	in contrast the king eider usually dived deeper than 20m
Bustnes & Lonne 1997	common eider	water depth			10	this species usually feeds on molluscs, crustacean and echinoderms in relatively shallow water (<10m)
Bustnes & Lonne 1997	common eider	water depth		7.4		the common eider fed between 1.7 and 4.1 times more than expected in the 0-10m depth zone, they slightly avoided the 10-20m depth zone and completely avoided water >20m deep. The mean diving depth of the common eider was 7.4m
Bustnes & Lonne 1997	king eider	water depth		20.4	40	The king eider avoided the 0-10m zone, used the 10-20m zone as expected given its availability and used the >20m depth zone slightly more than expected. Mean dive depth was 20.4m
Bustnes & Lonne 1997	king eider	water depth				our observations confirmed the assumption that king eider is one of the most deep-diving species of sea duck (3 refs)
Bustnes & Lonne 1997	common eider	water depth			33	diving for scallops in Norway (Brun 1971)

Bustnes & Lonne 1997	common eider	water depth			42	in St Lawrence Canada (Guillemette et al 1993). This observation shows that common eider are capable of diving as deep as king eider however, the fact that common eider usually avoid such depths suggests that they are not as well adapted for deep water feeding.
Cramp & Simmons 1977	common scoter	water depth		not more than 10-20m	20	
Cramp & Simmons 1977	common scoter	water depth		2.95	6.7	81% of dives in 2.2-3.7m
Cramp & Simmons 1977	common scoter	water depth			6.4	maximum
Cramp & Simmons 1977	common scoter	water depth		15		usual is 10-20m
Cramp & Simmons 1977	common scoter	water depth		14	30	maximum
Cramp & Simmons 1977	common scoter	water depth	1		3	normally in Iceland
Cramp & Simmons 1977	common scoter	water depth	1.5		3.5	preferred
Cramp & Simmons 1977	surf scoter	water depth			9	inshore marine waters rarely beyond 9m depth, often within zones of breaking waves, rests in flocks further out
Cramp & Simmons 1977	velvet scoter	water depth		5		normal foraging depth, occasionally much more
Cramp & Simmons 1977	velvet scoter	water depth	2	5	7	more rarely up to 7m (Finland)
Cramp & Simmons 1977	velvet scoter	water depth	14		30	Danish waters
de leeuw 1997	tuftie/pochard	water depth				is shallower in early winter than later
Degraer et al 1999	common scoter	water depth				groups of seaducks can be found on places where it is too deep to dive for food

Durinck et al 1993	common scoter	water depth		10		
Durinck et al 1993	velvet scoter	water depth			20	generally use waters less than 20m deep
Durinck et al 1993	scoters	water depth			20	most of the food items found belong to spp distributed in waters less than 20m deep
Fox 2003	scoters	water depth	5		15	preference in the Wadden Sea
Fox 2003	scoters	water depth		5.93		aerial survey results from the Kattegat, Denmark. Mean depth of water over which bird recorded fell in a predictable fashion through each of the winter months to reach a max depth of 9.4m by following April (depletion?????)
Fox 2003	scoters	water depth			9.4	aerial survey results from the Kattegat, Denmark
Fox 2003	scoters	water depth			20	only 0.015% of 568,000 scoters observed at positions with depths > 20m
Goudie & Ankney 1986	common scoter	water depth			15	
Guillemette 2001	common eider	water depth	0		12	the bulk of dives for both subspecies were in the depth range 0-3m
Guillemette et al 1993	common eider	water depth (m)		0-6		in both winters, the depth selectivity index was well in excess for the 0-6m depth range which supports the prediction that eiders strongly selected shallow habitats for feeding.
Guillemette et al 1993	common eider	water depth (m)			24-42	Even though the 24-42m depth range was significantly ignored for both winters, we observed eiders were capable of diving to such depths
Guillemette et al 1996	common eider	water depth			42	source Guillemette et al 1993
Guillemette et al 2004	common eider	water depth			3-5m	three out of 4 females dived mostly to depths <3m but one female dove up to depths of 5m

Guillemette et al 2004	common eider	water depth			6.5-9	for the 2 females followed over 9 months, diving occurred in deeper water in winter when most dives were <6m but reaching maxima of 9m for one female and 6.5m for another
Guillemette et al 2004	common eider	water depth			6	Our results are in general agreement with the few studies that have measured depth use in common eiders, which prefer to dive in the 0-6m depth range in eastern Canada (Guillemette et al 1993) and in northern Norway (Bustnes & Lonne 1997)
Guillemette et al 2004	common eider	water depth			42	source Guillemette et al 1993
Hawkins et al 2000	common eider	water depth			60	
Kirby et al 1993	velvet scoter	water depth			10	commonly feed at depths of less than 10m
Larsen & Guillemette 2000	common eider	water depth (m)		0-6		the highest concentrations of common eiders were found at shallow water depths. Eiders at Tuno Knob preferred to dive in 0-6m water depth despite 10 fold higher benthic biomass in deeper water (6-12m) (although this comprised large unprofitable mussels)
Larsen & Guillemette 2000	common eider	water depth (m)		6 to 20		large numbers of common eiders in the Arhus bay feed at these depths
Larsen & Guillemette 2000	common eider	water depth (m)			25-45	common eiders are known to dive at depths of 25-45m (Brun 1971, Guillemette et al 1993)
Leopold et al 2001	common eider	water depth	25		50	in Norway (two refs)
Leopold et al 2001	common eider	water depth				Larsen & Guillemette (2000) found that eiders very much prefer natural beds at water depths shallower than 6m than beds at 6-12m
Lovvorn & Gillingham 1996	canvasbacks	water depth	0.5		3.5	
Lovvorn & Gillingham 1996		water depth				several field studies have noted the importance of water depth in feeding site selection by diving ducks.

Lovvorn & Jones 1991	long-tailed duck	water depth			60	
Lovvorn & Jones 1991	common eider	water depth			60	
Lovvorn et al 2003	spectacled eider	water depth		40-70m		
Meissner & Brager 1990	common scoter	water depth	6		22	6-10m depths are of major importance to the ducks , although the significance of deeper water areas as feeding grounds (where Arctica islandica occurs) was not appreciated
Mitchell 1992	redhead	water depth				predicting redhead flock locations and amount of time spent there, based solely on the percent of time water was 12-30cm deep, accurately reflected where redheads were found
Nehls 2001	common eider	water depth			30	Bivalves are captured by head dipping or diving up to depths of 30metres
Nilsson 1972	velvet scoter	water depth	7		25	occurred in flocks of moderate size (10-25) well out at sea. Mainly found in areas with depths 7-25m over stony bottom with Mytilus edulis or over sand with Macoma balthica
Nilsson 1972	common scoter	water depth	7		25	only seen in small numbers and generally associated with the velvet scoters.
Nilsson 1972	velvet/common scoter	water depth		10m-15m	>20	the scoters stayed far out to sea and their diving habits could not be studied. During boat surveys diving scoters were seen at depths of more than 20m, normal depths being 10-15m
Owen et al 1986	common scoter	water depth		10	20	often in depths of 10-20m, though usually less than 10m
Owen et al 1986	velvet scoter	water depth		10	30	accomplished diver feeding at depths up to 30m though most commonly under 10m
Reynolds 1987	long-tailed duck	water depth		3m-10m	55	introductory comments gleaned from other sources

Richman & Lovvorn 2003	spectacled eider	water depth		40-70		
Stempniewicz 1986	scoters	water depth			30	depths down to which birds caught in fishing nets
Stott & Olson 1973	scoters	water depth	9		12	these were the depths in the areas where most seaducks (especially scoters) were observed
Systad & Bustnes 2001	stellers eider	water depth			5	90% of birds fed in waters <5m deep
Ydenberg & Guillemette 1991	common eider	water depth	0		15	

Appendix 7 Notes concerning individual variation between diving ducks

source	species	parameter	comments
Draulans 1984	tufted duck	individual variation	the calculated profitability curves were QUIITE DIFFERENT for the four ducks. The most profitable size class varied from mussels of 12.5-15mm to 20-22.5mm. This variation can only stem from variation in the speed with which different birds handled mussels of different sizes.
Draulans 1987	tufted duck	individual variation	the optimal mussel size curves indicate LARGE DIFFERENCES BETWEEN ALL INDIVIDUALS tested. The data suggest that individual variability in SKILL in dealing with mussels could be important in determining the shapes of optimality curves
Green et al 2005	various diving animals	individual variation	cites various studies on species ranging from little penguins to grey and Weddell seals that demonstrate individual variation in diving performance (depth, dive durations, stroke frequencies, descent speeds and surface durations)
Green et al 2005	various diving animals	individual variation	Juvenile diving animals COMMONLY show an improvement in their ability to dive during their development.(several refs)
Guillemette et al 2004	common eider	individual variation	we suggest that the large variation observed in the diving behaviour of female eiders reflects individual female DIVING CAPABILITY, which is probably related to their physiological states.
Guillemette et al 2004	Aythya app	individual variation	However, Carbone & Houston (1994) observed considerable variation in the behaviour of ducks, and for the purpose of their work, they removed that variation from their analysis.
Halsey et al 2003	tufted duck	individual variation	at the level of the individual duck, four of the model predictions for surface time in the control conditions were signif different from the observed values. All six predictions of oxygen consumption during foraging were signif different from the observed values. When a substrate was added to the food tray, all six of the model predictions of optimal surface time for individual ducks were significantly different from observed values and 4 of 6 predictions of oxygen consumption while foraging were also signif different from observed.
Halsey et al 2003	tufted duck	individual variation	The model appears to be fairly successful at predicting the average diving behaviour of a number of tufted ducks but was unsuccessful at doing so for individual birds. For a single animal, the model may not always incorporate all the parameters that are influential in determining its diving behaviour.

Halsey et al 2003	tufted duck	individual variation	In comparing the time budget data and the oxygen restock curves of the six birds there are arguably FOUR foraging strategies. The categorization is somewhat arbitrary but demonstrates the wide variation in behaviour within a species. Mean values derived from varied individuals generated to represent the behavioural strategy of a species are consequently misleading. Tufted ducks may have different optimal diving strategies because of their individual physiologies, or their strategies may be optimal under particular remembered conditions.
Hepp & Hair 1984	Anas spp	dominance	in intraspecific interactions, males dominated females when both were either paired or unpaired, but paired individuals dominated unpaired individuals regardless of sex. Early pair formation may be advantageous in wintering dabbling ducks because the resulting higher dominance may give better access to food. These results support the hypothesis that behavioural dominance influences differential distribution of males and females during the non-breeding season
Nehls 1995	common eider	individual variation	Fig 5.6 shows pronounced variation between 5 eiders in the relationship between mussel handling time and mussel length.
Tome 1988	ruddy ducks	individual variation	I compared the slopes and intercept of the energy gain functions among individual birds within a patch density and found NO DIFFERENCE in slopes or intercepts.
Tome 1988	ruddy ducks	individual variation	However, optimal foraging efficiency (in terms of when birds chose to leave patches) differed between individuals-some birds behaved closer to optimality than others

Appendix 8 Notes concerning the existence of interference competition between diving ducks

source	species	parameter	comments
Approp Asses 2005	common eider	interference	WILD mussel and cockle stocks that ARE ACCESSIBLE to eider are probably insufficient to support minimum mortality rates in eider. This is assuming similar interference competition occurs between eider as behavioural modelling has shown to occur between oystercatchers in the Wash
Approp Asses 2005	common eider	interference	assuming interference competition also occurs in eider ducks, the current natural mussel and cockle stocks (which amount to c 3 times the amount consumed by eider alone) are unlikely to be sufficient to support the eider population (because oystercatchers need 4-6 times the amount that they eat)
Ashcroft 1976	common eider	interference	The plot shows a significant linear negative relationship between feeding rate and the number of displays. Interactions with other birds have the effect of lowering the female's feeding rate
Ashcroft 1976	common eider	interference	Comparing the mean feeding rate (items/min) achieved by female eiders in medium density flocks (2.62items/min) and high density flocks (2.20 items/min) there is a 16% drop in achieved feeding rate with increasing density. 2.62 is the highest mean value given in Table 1 for any flock density (isolated birds do worse) and is also very near the intercept of the regression equation fitted between feeding rate and displays per female per minute ie 2.68 at 0 displays which might approximate an IFIR). Thus maybe one could take 2.62 as an IFIR and say that at the highest flock densities this will be reduced by 16%. Need to check how this compares to oystercatchers across the observed range of densities.
Christensen 2000	common eider	pair formation	pair formation in the eider takes place in LATE AUTUMN AND EARLY WINTER. This early pair formation is assumed to secure female foraging through REDUCED INTERFERENCE from conspecifics throughout winter and spring (3 refs)
de Leeuw 1997	diving ducks	interference	although interspecific aggressive behaviour is rarely observed in free living ducks the segregation of the species might well be a result of interference competition….this phenomenon can also explain the tendency for segregation between males, females and juveniles within the species

Giles 1990	tufted duck(lings)	interference	I have not observed any instances of intraspecific aggression either within or between broods of tufted ducklings which could reduce foraging efficiency either under natural conditions or in the lab.
Guillemette & Himmelman 1996	common eider	interference	Eiders crowd increasingly into 1 or 2 favoured patches (rather than spreading out over all 13 patches) as population density increased. We thus discarded the possibility that interference was driving the distribution of wintering eiders.
Guillemette & Himmelman 1996	common eider	interference	to distinguish between the ideal free and allee type distributions, one requires knowledge on the relationship between feeding rates and eider density over a patch AND THIS IS BEYOND THE SCOPE OF THIS STUDY
Guillemette & Himmelman 1996	common eider	interference	The number of patches used by eiders was not influenced by the overall density of eiders in the mussel bed habitat (which varied from 10 to a few thousand birds). On two out of 159 surveys, 4 patches were used simultaneously but in 80% of the surveys only 1 or 2 patches were used. (One can estimate from the max eider count categories in Fig 1 i.e. 3200 and the size of the 2 most popular beds (see Table 1) ie 4.67ha that a reasonably likely estimate of the maximum observed density of eiders across the 2 beds used at high population sizes was c 685birds/ha. (Assuming that the two most preferred beds were the ones used predominantly when the population was big).This lack of spreading out and indeed tendency to continue to use only c 2 patches out of the 13 available regardless of population size may be consistent with the tendency of eiders in the Wash to concentrate on Roger and Toft lays only - and may mean that a high degree of aggregation in the model predictions can be accepted.

Guillemette & Himmelman 1996	common eider	interference	The number of patches used by eiders in a given survey DOES NOT increase with an increase in population density. The eider flocks did not disperse evenly over food patches but almost always fed in tight rafts over a part of it. This suggests that the critical density threshold at which interference competition occurs had not been reached (NB perhaps c685birds/ha is not high enough?). Goudie & Ankney (1988) measured the aggressive behaviour of common eiders in winter and FOUND IT WAS NEGLIGIBLE compared to other seaduck species. Indeed observations of foraging behaviour of eider (Guillemette et al 1992) indicate that interference competition is absent when eiders are searching for blue mussels in kelp beds. Interestingly, interference competition arises and takes the form of intraspecific kleptoparasitism when they forage in Agarum beds for spider crabs a rare prey species of a high energetic value (and long handling time I guess). In light of this we reject the hypothesis that population density and interference competition influence the distribution of common eiders. We suggest that the high level of crowding in given surveys and low importance of interference competition in this species is related to the high abundance of their preferred food resources (small mussels (mean 6.5mm) occurred at an average density of 25,000 per sq m or 2.8kg wet mass per sq m at the start of winter)
Guillemette & Himmelman 1996	common eider	interference	When feeding on (small) mussels, common eiders can be considered as grazers rather than real predators. This decreases the potential for interference competition. That eiders increasingly crowd over a few patches as their density increases indicates that their distribution may conform to an Allee-type distribution. In this type of distribution, habitat profitability increases with population density up to a certain point because the benefits of aggregation are greater than the costs. However, without knowing the relationship between eider feeding rate and flock size, the idea that wintering eiders conform to an allee-type distribution remains speculative.
Guillemette & Himmelman 1996	common eider	interference	Irrespective of population density, eiders only use a small number of patches relative to the number of patches present (ie 2-3 out of 13)
Guillemette et al 1993	common eider	interference	In winter, common eiders are highly social animals. They are not aggressive and feed in tight rafts

Guillemette et al 1993	common eider	interference	although the reef habitat is the PREFERRED habitat throughout the winter, the degree to which it is selected varies greatly with season and population size. Exploitative competition and prey depletion may explain this pattern of habitat selection. In some birds, an increase in population size is associated with increased interference competition which leads to the dispersion of individuals (Ens & Goss-Custard 1984). In winter, common eiders composing a flock feed in tight rafts and are not aggressive (Campbell 1978, Goudie & Ankney 1988). Guillemette (1991 thesis) demonstrated that the number of reef patches used DOES NOT INCREASE with population density and thus **HE DISCARDED THE POSSIBILITY THAT INTERFERENCE COMPETITION WAS DRIVING THE DISTRIBUTION OF EIDERS.** that eiders increasingly crowd into a few reef patches as population size increases indicates rather that the benefits of aggregation are equal to or greater than the costs
Hart & Brown 2006	common eider	dominance hierarchy	adult males dominate the food resources (and in normal populations are typically 1.5 times more abundant than females and juveniles). (Furness pc). Foraging conditions were likely to be best where the males predominated and worst where females and juveniles predominated. Males predominated on the Roger lay (less disturbed) and the proportion found there only declined after the mussels were dredged up. In contrast, on the Toft lays where there was more disturbance and perhaps less competition for foraging space (because less favoured), females and juveniles predominated. This big difference between the two lays persisted throughout the study even as the overall % males in the population changed.
Hohman 1993	canvasbacks	interference	aggression associated with feeding was commonly observed in wintering canvasbacks
Hohman 1993	canvasbacks	interference	this difference might have resulted from INTERFERENCE competition with adults.
Hohman 1993		interference	competition between the sexes and age classes during winter is assumed to be deleterious to females and immatures, however, effects of competition on survival and reproductive performance have not yet been demonstrated.
Leopold 2002	common eider	interference	the birds showed some aggression (behind the boat discarding by catch) , particularly when one surfaced very close to another; one would then be chased about half a meter. Birds surfacing with large prey often turned their backs to the flock and swam away handling the prey, but no actual intraspecific kleptoparasitism was seen. NB this was a very artificial and highly competitive foraging situation.

Lovvorn & Gillingham 1996	canvasbacks	interference	foraging canvasbacks are often displaced from profitable loci by other individuals that observe their success
Nehls & Ketzenberg 2002	common eider	interference	social interactions limit the density of feeding eiders on their preferred feeding grounds below a level which would lead to prey exhaustion
Nehls & Ketzenberg 2002	common eider	interference	a negative effect of density on the food intake has indeed been found in Scottish eiders
Nehls & Ketzenberg 2002	common eider	interference	although eiders may gather in large and dense flocks, interference within these groups apparently is higher than in other waterfowl eg geese. In the Wadden sea, aggressive interactions between feeding or resting eiders occur frequently
Nehls 1989	common eider	interference	since oystercatchers preferably feed on rather high mudflats close to their roosts there seems to be little interference with eiders
Nehls 1995	common eider	interfernce	social interactions appeared to limit the densities of foraging eiders on the preferred feeding grounds page 155
Piersma & Camphuysen 2001	common eider	interference	we put forward the hypothesis that gross overfishing…resulted in permanently reduced food resources, a reduced foraging area and an increased use of secondary prey such as Spisula all of which led to INCREASED INTERFERENCE COMPETITION AMONG EIDERS
Piersma & Camphuysen 2001	common eider	interference	combined fisheries activities in the Wadden Sea seem to have resulted in a reduction of the foraging range of eiders by the removal of old natural mussel banks, the partial removal of high density cockle and Spisula banks and a shift towards (concentrated?) mussel cultures. This would then have led to increased levels of interference and a reduction in the carrying capacity of the Dutch WS
Rodway & Cooke 2001	harlequin duck	group sizes	group sizes near shore were much larger during the herring spawning period than at other times (ie 1656-3172 birds cf 4-283 birds at other times). Suggests far greater aggregation when food is super abundant than is otherwise the case.
Schenkeveld & Ydenberg 1985	surf scoter	interference	we commonly observed glaucous winged gulls stealing mussels from diving birds. By attacking them as they surface from foraging dives.
Suter & Van eerden 1992	tufted ducks and pochards	interference	we suggest that competitive performance at a specific and often reduced food resource has much more influence on sex-related and interspecific differences in vulnerability to starvation than fat reserves built up prior to cold spells

Swennen et al 1979	common eider	interference	Sex ratios vary with the packing of the group. The percentage of males in the densely populated parts of offshore congregations was higher than in the sparsely populated areas.

Appendix 9 Notes concerning the diet and sizes of prey consumed by eiders

source	species	location	taxonomic group eaten	species eaten	min size (mm)	size(mm)	max size (mm)	comment
Bustnes & Erikstad 1988	common eider	northern Norway	fish	eggs of lumpsucker				important (25.9% of gullet contents (wet weight) but present in only 14.6% of birds
Bustnes & Erikstad 1988	common eider	northern Norway	bivalves	Mytilus edulis				dominant: 46.3% of gullet contents (wet weight) and present in 80.5% of all birds
Bustnes & Erikstad 1988	common eider		bivalves	Mytilus edulis				the dominance of M edulis in the common eider diet has been described in a large number of studies from most of the distribution range. It is also evident that M edulis forms the bulk of the diet during ALL seasons but it is probably most important in winter, spring and summer whereas crustaceans are more common in the diet in August to October (Penthon 1967)
Bustnes & Erikstad 1988	common /king eiders	northern Norway	crustacea					were eaten in small numbers by both common and king eiders
Bustnes & Erikstad 1988	common eider	northern Norway	echiniodermata					minor importance
Bustnes & Erikstad 1988	king eider	northern Norway	echinodermata					dominant (67.8% wet wt)
Bustnes & Erikstad 1988	king eider	northern Norway	molluscs					king eiders ate the same species of molluscs as common eiders but in much smaller quantities (62.4% in common eider v 22.8% in King eider)
Bustnes & Erikstad 1988	common eider							Common eiders are however opportunistic and their diet varies according to the availability of different prey species.
Bustnes & Erikstad 1990	common eider	Norway	bivalves	Mytilus edulis	3.5	13.9	38.1	
Bustnes & Erikstad 1990	common eider	Norway	bivalves	Mytilus edulis				% by occurrence
Bustnes & Erikstad 1990	common eider	scotland	bivalves	Mytilus edulis		23		
Bustnes & Erikstad 1990	common eider	scotland	bivalves	Mytilus edulis			>40	65%

Bustnes & Erikstad 1990	common eider	denmark	bivalves	Mytilus edulis		30-40		
Bustnes & Erikstad 1990	common eider	england	bivalves	Mytilus edulis	19		60	
Bustnes & Erikstad 1990	common eider							common eiders select mussels below the mean size found in the mussel beds (refs) as do other duck spp (ref)
Bustnes & Erikstad 1990	common eider							eiders select (smaller) mussels to minimise the ratio of shell to flesh weight in their daily intake of food
Bustnes & Galaktionov 2004	common eider		crustacea					we suggest that avoiding the risk of being parasitized may be an important determinant of prey choice in other sea ducks as well, and may explain why such birds usually have low proportions of crustaceans in their diets. For example, in the common eider, crabs are a minor part of the diet even if they have a high energy density compared with shelled prey (Guillemette et al 1992). However, some crabs are intermediate hosts of acanthocephalans eg Polymorphus botulus.
Bustnes 1998	common eider							the results of this study strongly indicate that reducing the amount of indigestible shell is an important factor for eiders selecting among mussels of different lengths
Bustnes 1998	common eider							Length had a highly significant effect on the % of mussels eaten within 6 size classes (negative).
Bustnes 1998	common eider							Nehls 1995 showed that eiders selected large mussels (55mm) during winter but during the summer after the large mussels had spawned (much higher relative shell content) they fed predominantly on the smaller non-spawning mussels
Dunthorn 1971	common eider	Argyll	bivalves	Mytilus edulis	19		34	27-30mm commonest size (from rope cultured mussels) (based on 34 mussels in a drowned bird)
Dunthorn 1971	common eider	Argyll	bivalves	Mytilus edulis			52-60	based on only 4 mussels in a shot bird
Guillemette 1994	common eider	St Lawrence	bivalves	Mytilus edulis		9.7		

Guillemette 1998	common eider	Canada	bivalves	Mytilus edulis		8		in both cases, eiders consume mussel sizes in proportion to those in the environment
Guillemette 1998	common eider	St Lawrence	bivalves	Mytilus edulis		8		modal length
Guillemette 1998	common eider	St Lawrence	bivalves	Mytilus edulis		9		in both this case (Guillemette et al 1996) and that of Nehls (1992) eiders consumed mussel sizes in proportion to those in the environment
Guillemette 1998	common eider	Wadden sea	bivalves	Mytilus edulis		42		in both this case (Nehls 1992) and that of (Guillemette et al 1996) eiders consumed mussel sizes in proportion to those in the environment
Guillemette 1998	common eider	Wadden sea	bivalves	Mytilus edulis		42		in both cases, eiders consume mussel sizes in proportion to those in the environment
Guillemette 1998	common eider	Canada	bivalves	Mytilus edulis		9		in both cases, eiders consume mussel sizes in proportion to those in the environment
Guillemette 1998	common eider	Norway	bivalves	Mytilus edulis		13		
Guillemette et al 1992	common eider	Canada	bivalves	Mytilus edulis	1	7-8(mode)	25	highly preferred over sea urchins
Guillemette et al 1992	common eider	Canada	echinodermata	sea urchins	10		46	not preferred at all
Guillemette et al 1992	common eider	Canada	crustacea	spider crab	30		51	highly preferred over sea urchins
Guillemette et al 1996	common eider	St Lawrence	echinodermata	green sea urchins	10		46	% by wet mass
Guillemette et al 1996	common eider	St Lawrence	bivalves	Mytilus edulis	1		25	% by wet mass

Guillemette et al 1996	common eider	St Lawrence	bivalves	Mytilus edulis	2		60	possible size range for eiders
Hamilton 2000	common eider	Canada	bivalves	Mytilus edulis		11-25mm		the abundance of mussels declined, particularly in the 11-25mm size range in plots where ducks fed. These sizes correspond to preferred size classes of mussels selected by ducks during most of the year (Hamilton et al 1999)
Hamilton et al 1999	common eider							preferred smaller mussels than those that would have been the most energetically profitable. During most of the year (spring summer and autumn) they select relatively small mussels that MINIMISED SHELL INGESTION. In winter, differences among length classes in shell ingestion became small and birds switched to feeding on larger prey that provided more energy per unit work and probably were more profitable.
Hamilton et al 1999	common eider				10		50	all classes were within the range ducks were physically capable of taking (Hamilton 1997)
Hamilton et al 1999	common eider							for most of the year, ducks selected prey that allowed them to MINIMISE SHELL INGESTION when large differences between shell length classes were evident. However, when shell mass was least variable among mussel length classes, common eiders appeared to switch tactics in an attempt to maximise short term energy intake by taking large mussels (when really pushed for energy???)
Hamilton et al 1999	common eider							energy INTAKE maximisation appears NOT to be the primary factor influencing prey selection by common eider (although maybe maximisation of assimilated energy is given the higher efficiency with which they can probably digest meals consisting of a lower % of shell??)
Hamilton et al 1999	red knot							birds selected Macoma balthica that minimised shell intake relative to the amount of tissue ingested.
Hario & Ost 2002	common eider	wadden Sea	bivalves	Macoma balthica				tellins are burrowing clams…. They also seem to be an energetically poor substitute for mussels and are directly avoided by eiders in areas with access to

								mussel beds (Hilgerloh 2000)
Hario & Ost 2002	common eider	Finland	bivalves	Mytilus edulis	3.6		>19	the biomass of mussels was calculated excluding those belonging to the smallest size class ie 1.8-3.5mm
Hilgerloh 1997	common eider	Wadden sea	bivalves	Mytilus edulis				The share of blue mussels in the food of eiders was assumed to amount to 80% in a year with high predation on blue mussels and to 68% in a year with low predation on blue mussels, following a 2yr study in 1993 and 1994 at the study site (Hilgerloh in press)
Larsen & Guillemette 2000	common eider				3		80	although eiders have been found to take bivalves as small as 1mm, the most frequent prey sizes are >3mm (Madsen 1954). 80mm is the maximum size of prey eaten by the common eider (Cottam 1939, Madsen 1954)
Leopold et al in press	common eider	North Sea	bivalves	Ensiis americanus				was present in 87 out of 92 droppings (94.7%) and 78.3% of the samples contained Ensis exclusively. Ensis americanus was the staple food
Leopold et al in press	common eider	North Sea	bivalves	Ensiis americanus	41		64	in December 2001 - based on hinge measurement analyses
Leopold et al in press	common eider	North Sea	bivalves	Ensiis americanus	53		140	in February 2003 - based on hinge measurement analyses
Leopold et al in press	common eider	North Sea	bivalves	Ensiis americanus	45		80	in December 2001 - based on shell thickness measurement analyses
Leopold et al in press	common eider	North Sea	bivalves	Ensiis americanus	66		108	in February 2003 - based on shell thickness measurement analyses
Leopold et al in press	common eider	North Sea	bivalves	Ensiis americanus				when given the choice between 0 group and 1 group Ensis, eiders clearly selected the larger 1 group prey Ensis of 80-90mm. There is some evidence that eiders and scoters are capable of eating even larger Ensis.
Leopold et al in press	common scoter	North Sea	bivalves	Spisula subtruncata	12		29	there is a suggestion that Spisula of 25-30mm were taken disproportionately often (the bulk of available prey items being 14-21mm). According to Fox (2003) this is the first direct evidence for size selection by scoters.

Leopold et al in press	common eider							in contrast to common scoters, many studies on the feeding ecology of common eider have shown that these birds are selective, taking mussels sizes with the highest energy return or prefer small or thin shelled individuals or mussels with few barnacles attached.
Leopold 2002	common eider	Wadden sea	bivalves	Cerastoderma edule			39.5	source Nehls 1991.
Leopold 2002	common eider		bivalves	Cerastoderma edule			49	Swennen (1976) also found in feeding experiments that eiders strongly selected against cockles larger than 40mm long, although they could ingest cockles up to 49mm
Leopold 2002	common eider	Wadden sea	bivalves	Ensiis americanus			120	Ensis up to 120mm were seen to be swallowed behind the boat. Eiders have been noted to take large Ensis in considerable numbers without the help of fisherman (in Norway and Denmark (refs))
Leopold 2002	common eider	Wadden sea	bivalves	Mya arenaria				both the clam Mya arenaria and several species of polychaete worms, abundant and widespread throughout the Wadden Sea are used as food by many other birds but SEEMINGLY not by eiders. Several studies in the Baltic have shown that Mya and Neries diversicolor are potential prey for eiders (refs). Several studies found these prey in eider but interestingly in their stomachs rather than their faeces.
Leopold 2002	common eider	Wadden sea	bivalves	Mya arenaria			75	shell width, height or circumference may be more important in determining the maximum size that can be swallowed. The largest Mya that could be forced through a dead eiders gape was 75mm long
Leopold 2002	common eider	Wadden sea						studies of faeces contents may give a highly biased impression of local eider diet
Leopold et al 2001	common eider	Wadden Sea	echinodermata	Asterias rubens				supplementary food items

Leopold et al 2001	common eider		echinodermata	Asterias rubens				ARE EATEN REGULARLY PERTICULARLY ON SUBLITTORAL MUSSEL BEDS AND CULTURE LOTS. Unclear is just by-catch or selected. One study found starfish and crabs to be the dominant prey in winter indicating that such prey gain importance when mussels reach a low flesh content at that time of year ie ALTERNATIVE PREY
Leopold et al 2001	common eider	Wadden Sea	crustacea	Carcinus maenas				supplementary food items
Leopold et al 2001	common eider		crustacea	Carcinus maenas				Crabs are regularly taken by most eiders in the Wadden Sea. Eating crabs is often seen as a sign of poor feeding capability, and mostly observed in juvenile or inexperienced birds that feed in shallow near shore waters, or as a sign of a lack of more suitable food (Camphuysen et al subm). Laursen et al (MS) found crabs in the stomachs of juvenile eiders in particular suggesting that adult birds prefer or are better able to feed on other prey i.e. mussels and cockles
Leopold et al 2001	common eider	Wadden Sea	bivalves	Cerastoderma edule				staple diet in all major diet studies within the Wadden Sea
Leopold et al 2001	common eider		bivalves	Cerastoderma edule				even less is known about size selection in cockles. There are no field studies that compare cockles taken with those locally present.
Leopold et al 2001	common eider		bivalves	Cerastoderma edule	5		50	these are the absolute minimum min and maximum max length values of cockles taken by eiders across an overview of studies (see Fig 3)
Leopold et al 2001	common eider		bivalves	Cerastoderma edule	15		40	these are the most frequently recorded minimum and maximum recorded lengths of cockles taken by eiders across an overview of studies (see Fig 3)
Leopold et al 2001	common eider		bivalves	Ensis directus				they are apparently eaten in certain situations. Laursen et al (MS) found that Ensis constituted over 50% of all prey items in one of their study areas
Leopold et al 2001	common eider	Wadden Sea	gastropoda	Hydrobia ulvae				too small to be profitable

Leopold et al 2001	common eider	Wadden Sea	gastropoda	Littorina littorea				supplementary food items
Leopold et al 2001	common eider		gastropoda	Littorina littorea				rarely considered as an important food source . In one study in Canada periwinkles found to be important prey to juvenile eiders (Cantin et al 1974). For the Wadden Sea there is also some evidence that at least some individuals may focus on this prey, possibly those birds that are heavily parasitized (Swennen 1976). There is some anecdotal evidence that in times of food shortage more eiders may switch to eating periwinkles (refs). Littorina is probably eaten in the high intertidal zone and on rocky shores ie on dikes at the edges of the WS WHERE JUVENILE AND SICK EIDERS ARE MOST ABUNDANT (SWENNEN 1976).
Leopold et al 2001	common eider	Wadden Sea	bivalves	Macoma balthica				supplementary food items
Leopold et al 2001	common eider		bivalves	Macoma balthica				only once found as an important food source (Laursen et al MS). Many Macoma will be too small to be profitable and most of the larger animals live relatively deeply in the sediment, especially in winter (ref). On top of this, large Macoma are very hard shelled and thus take a relatively high amount of energy to be broken in the bird's stomachs (Camphuysen et al submitted)
Leopold et al 2001	common eider		bivalves	Mya arenaria				quickly become unsuitable as prey as they become too deeply buried and too large to swallow. We know very few studies where feeding on Mya was observed on more than a very limited scale.
Leopold et al 2001	common eider		bivalves	Mytilus edulis	<10			in kelp dominated areas (St Lawrence, Canada)
Leopold et al 2001	common eider		bivalves	Mytilus edulis	10		40	in northern Norway and the Baltic and Wadden Sea areas
Leopold et al 2001	common eider		bivalves	Mytilus edulis			70	in the Wadden Sea

Leopold et al 2001	common eider		bivalves	Mytilus edulis				eiders usually focus on bivalve molluscs and on blue mussels in particular. In most situations, at least one other prey species is also important. In the Wadden Sea, cockles fill this role. It is unknown to what extent other prey species might supplement the diet when both primary species are scarce.
Leopold et al 2001	common eider	Wadden Sea	bivalves	Mytilus edulis				staple diet in all major diet studies within the Wadden Sea
Leopold et al 2001	common eider	Wadden Sea	bivalves	Mytilus edulis				In the WS, subtidal cultured mussels are the most profitable (Camphuysen et al subm) and therefore the vast majority of eiders in the Dutch WS reside over these mussels if they are available.
Leopold et al 2001	common eider	Wadden Sea	bivalves	Mytilus edulis				mussels on culture lots have thinner shells and are less well attached to each other than intertidal ones and so should be the preferred food of eiders (three refs)
Leopold et al 2001	common eider		bivalves	Mytilus edulis				Nehls (1995) agrees with the suggestion that the size of ingested mussels increases during the winter but this may be due to energetics rather than simply depletion of the preferred smaller ones. Subtle differences in flesh contents and shell masses between different size classes govern the birds' feeding decisions over winter.
Leopold et al 2001	common eider		bivalves	Mytilus edulis	0-5		80-85	these are the absolute minimum min and maximum max length values of mussels taken by eiders across an overview of studies (see Fog 1 bottom)
Leopold et al 2001	common eider		bivalves	Mytilus edulis	25		50	these are the most frequently recorded minimum and maximum recorded lengths of mussels taken by eiders across an overview of studies (see Fog 1 bottom)
Leopold et al 2001	common eider	Wadden Sea	bivalves	Mytilus edulis		20-50		in summer (Nehls 1995)
Leopold et al 2001	common eider	Wadden Sea	bivalves	Mytilus edulis		40-70		in winter (Nehls 1995)

Leopold et al 2001	common eider	Wadden Sea	bivalves	Mytilus edulis		30-50		Laursen et al (MS) found that shot birds in Denmark the mussels taken (30-50mm) differed from those available (5-70mm) indicating that eiders did not select ie avoided both the smallest and largest mussels. However, if the mussels on offer were on average small (<30mm) the eiders selected the largest mussels available (30-50mm)
Leopold et al 2001	common eider	Wadden Sea	bivalves	Spisula subtruncata				new and important prey species for eiders in the Netherlands. Camphuysen et al (subm) showed that Spisula can be a profitable prey spp provided that large specimens can be eaten. Eiders were shown to be able to live only on large (>15mm, preferably even >25mm) specimens
Leopold et al 2001	common eider		bivalves	Spisula subtruncata	10 to 15			size selection has not been directly studied.. However, eiders always selected sites with the largest Spisula. Spisula smaller than 10-15mm seem to be too small.
Leopold et al 2001	common eider		bivalves	unidentified clams			54	in Norway
Leopold et al 2001	common eider		bivalves					for these reasons, Swennen (1976) considered that eiders prefer relatively small and smooth and hence safe prey.
Leopold et al 2001	common eider		bivalves					Larsen & Guillemette (2000) and Leopold et al (200) found evidence that depth at which prey occurs may also be limiting and that depth interplays with prey size.
Leopold et al 2001	common eider	Wadden Sea	polychates					most of the very abundant worm species are of very little importance to eiders
Leopold et al 2001	common eider							they usually specialise on one or more prey species in any one situation and the list of known prey species is long
Leopold et al 2001	common eider							most prey sizes can be taken by eiders but they seem to prefer MEDIUM SIZED PREY

Lovvorn & Gillingham 1996	common eiders, tufted ducks and common pochards							common eiders, tufted ducks and common pochards choose mussels of intermediate size both in the field and in the lab to minimise the mass fraction of shell, avoid taking items too large to swallow, reduce variations in profitability or to decrease competition with other diving duck spp.
Lovvorn et al 2003	spectacled eider							prey consumed elsewhere by spectacled eiders (snails amphipods other bivalve spp) were also common in the benthos but were not eaten
Lovvorn et al 2003	spectacled eider							prey consumed elsewhere by spectacled eiders (snails amphipods other bivalve spp) were also common in the benthos but were not eaten
Lovvorn et al 2003	spectacled eider							the rarity of Nucula bellotti in the birds relative to the grab samples suggests that the few thick-shelled N bellotti were ingested accidentally
Lovvorn et al 2003	spectacled eider							the rarity of Nucula bellotti in the birds relative to the grab samples suggests that the few thick-shelled N bellotti were ingested accidentally
Lovvorn et al 2003	spectacled eider							eiders selected N. radiata of 18-24mm (this size class was far more common in the diet in % number terms than it was in the benthic samples. Eiders ate few if any small specimens despite their high abundance. The largest size class 24-30 was rare in the benthos and in the birds' diet but was more prevalent in the birds than in the benthic samples - ie birds take the bigger size classes. The consumption of N radiata in greater proportion than available, the lack of other prey taken and selection by length class suggest that eiders developed a search image for N radiata of 18-24mm long.
Lovvorn et al 2003	spectacled eider							The much thicker shell of N bellotti probably requires more energy to crush in the gizzard. This factor appears to outweigh the importance of energy content per g (incl shell) which averaged 44% higher in N. b than in N rad of the same length (6-18mm). M calcarae was much less abundant than N. rad and also live deeper in the sediment.

Lovvorn et al 2003	spectacled eider							The much thicker shell of N bellotti probably requires more energy to crush in the gizzard. This factor appears to outweigh the importance of energy content per g (incl shell) which averaged 44% higher in N. b than in N rad of the same length (6-18mm). M calcarae was much less abundant than N. rad and also live deeper in the sediment.
Lovvorn et al 2003	spectacled eider							spectacled eiders consume a wide variety of prey under diff circumstances. This flexibility highlights the apparent selection of N radiata in this study while other viable prey were present.
Lovvorn et al 2003	spectacled eider							spectacled eiders consume a wide variety of prey under diff circumstances. This flexibility highlights the apparent selection of N radiata in this study while other viable prey were present.
Lovvorn et al 2003	spectacled eider							N. radiata eaten by spectacled eiders were of intermediate length. Several studies have shown size selection of bivalves by diving ducks and especially common eider eating mussels. Size selection has been explained by differential handling times, effects on meat/shell ratios on nutrient gain relative to passage rates or as a means of avoiding the risk of ingesting prey that are too large.
Lovvorn et al 2003	spectacled eider							Eiders probably consumed N radiata of intermediate length because most of the biomass was in that range and because energy intake per unit handling time (profitability) was greater than for smaller clams.
Nehls & Ketzenberg 2002	common eider	Wadden Sea	bivalves	Mytilus edulis	5	30-55	63	80% between 30-55mm
Nehls & Ruth 1994	common eider		bivalves	Mytilus edulis			65	mussels up to 65mm form an important part of the eider's diet in most areas

Nehls & Ruth 1994	common eider	Wadden Sea	bivalves	Mytilus edulis				recent observations indicate that over the last winters mussels were of higher importance than previously estimated and probably reached a share of 50% of the diet.
Nehls & Ruth 1994	common eider	Wadden Sea	bivalves	Mytilus edulis		30-55		tend to be selected in the Wadden Sea (median 45-50 in winter and 35-40 in early summer)
Nehls & Ruth 1994	common eider	Wadden Sea	bivalves	Mytilus edulis		30-55		the length distribution of the mussels determines the suitability of mussel beds or cultures for eiders. The high proportion of eiders found on mussel cultures in 1991 and 1992 coincides with the subtidal mussel stock reaching a length preferred by eiders (30-55mm mostly), in contrast to 1990 when mussels on the cultures were small (8-28mm) and few eiders utilised these places. However, this situation is not consistent over all years. in 1988 and 1989 when the mussels on the cultures were of similar size as in 1991 and 1992, but natural stocks of mussels were higher than during 1991 and 1992, few eiders were seen on mussel cultures
Nehls 1989	common eider	Wadden sea	bivalves	Cerastoderma edule				most important food items
Nehls 1989	common eider	Wadden Sea	bivalves	Cerastoderma edule				40% of the food in the Dutch Wadden Sea
Nehls 1989	common eider	Wadden Sea	bivalves	Cerastoderma edule				75% of the food during the summer in Schleswig Holstein
Nehls 1989	common eider	Wadden Sea	bivalves	Cerastoderma edule		30		within the preferred size range
Nehls 1989	common eider	Wadden sea	bivalves	Mytilus edulis				most important food items
Nehls 1989	common eider	Wadden Sea	bivalves	Mytilus edulis				40% of the food in the Dutch Wadden Sea
Nehls 1989	common eider	Wadden Sea	bivalves	Mytilus edulis		20-30		preferred
Nehls 1989	common eider	Wadden sea	other	various				shorecrabs, baltic tellins, mya arenaria, periwinkles and seastars are only of minor importance
Nehls 1995	common eider	Konigshafen	eel	Anguilla anguilla				Table 8.1 Konigshafen dietary item list

Nehls 1995	common eider	Konigshafen	echiniodermata	Asterias rubens				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Konigshafen	crustacea	Balanidae				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Konigshafen	crustacea	Carcinus maenas				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Konigshafen	bivalves	Cerastoderma edule				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Konigshafen	gastropoda	Crepidula fornicata				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Konigshafen	echiniodermata	Echinoidea				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Konigshafen	bivalves	ensis directus				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Konigshafen	crustacea	Eupagurus bernhardii				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Konigshafen	fish	flatfish spp.				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Konigshafen	oligochaete	Lanice conchilega				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Konigshafen	gastropoda	Littorina littorea				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Konigshafen	bivalves	Macoma balthica				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Wadden sea	bivalves	Mytilus edulis		30-55mm mainly		Fig 5.1. Size selected varies throughout the year. They mainly take mussels 30-55mm in length. Size selection varied seasonally. In spring they take smaller mussels with a narrower range than in autumn and winter.
Nehls 1995	common eider	Wadden sea	bivalves	Mytilus edulis	3		68	Fig 5.2
Nehls 1995	common eider	Wadden sea	bivalves	Mytilus edulis	17		69	Fig 5.2
Nehls 1995	common eider	Wadden sea	bivalves	Mytilus edulis	23		54	Fig 5.2
Nehls 1995	common eider	Wadden sea	bivalves	Mytilus edulis	5		54	Fig 5.2
Nehls 1995	common eider	Ostsee	bivalves	Mytilus edulis		15		Table 5.6 These are mean lengths taken
Nehls 1995	common eider	Ostsee	bivalves	Mytilus edulis		22		Table 5.6 These are mean lengths taken
Nehls 1995	common eider	Ostsee	bivalves	Mytilus edulis		20		Table 5.6 These are mean lengths taken
Nehls 1995	common eider	Ostsee	bivalves	Mytilus edulis		15-21		Table 5.6 These are mean lengths taken
Nehls 1995	common eider	Ostsee	bivalves	Mytilus edulis		17		Table 5.6 These are mean lengths taken
Nehls 1995	common eider	Tromso	bivalves	Mytilus edulis		14		Table 5.6 These are mean lengths taken

Nehls 1995	common eider	St Lawrence	bivalves	Mytilus edulis		10		Table 5.6 These are mean lengths taken
Nehls 1995	common eider	Ythan	bivalves	Mytilus edulis		18		Table 5.6 These are mean lengths taken
Nehls 1995	common eider	Firth of Forth	bivalves	Mytilus edulis		15-25		Table 5.6 These are mean lengths taken
Nehls 1995	common eider	Wattenmeer	bivalves	Mytilus edulis		31-44		Table 5.6 These are mean lengths taken
Nehls 1995	common eider	Konigshafen	bivalves	Mytilus edulis		32-53		this study Table 5.6 These are mean lengths taken
Nehls 1995	common eider	Konigshafen	bivalves	mytilus edulis				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Konigshafen	oligochaete	Nereis virens				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Konigshafen	bivalves	Venerupis pullastra				Table 8.1 Konigshafen dietary item list
Nehls 1995	common eider	Konigshafen				40		this is the median mussel size selected by eiders in August 1992 which turns out to be that which minimises the rate of daily energy expenditure needed to acquire a given energy gain ie the most efficient size to feed on. Fig 5.17
Nehls 2001	common eider		bivalves	Cerastoderma edule				these do NOT grow outside the size range consumed by eiders SO ALLOW ALL COCKLES IN THE MODEL TO BE EATEN. They do tend to prefer the larger ones (Nehls 1991)
Nehls 2001	common eider		bivalves	Mytilus edulis		40-50	60	in winter this was the median size taken but eiders did take a wide size range. Mussels larger than 60mm were rarely taken.
Nehls 2001	common eider		bivalves	Mytilus edulis				in late spring a sharp drop occurred in the size of mussels consumed. In May the smallest available mussels were taken and eiders focussed on a narrow range of sizes
Nehls 2001	common eider		bivalves	Mytilus edulis	30		50	80% of the mussels consumed were between 30 and 52mm
Nehls 2001	common eider		bivalves	Mytilus edulis			80	eiders are able to consume mussels up to 80mm
Nehls 2001	common eider		bivalves	Mytilus edulis				eiders which fed at low tide by head dipping and eiders feeding at high tide by diving on the mussel bed consumed the same size ranges
Nehls et al 1997	common eider	Wadden Sea	bivalves	Cerastoderma edule				during October and November, 50% of their diet consists of cockles

Nehls et al 1997	common eider	Wadden Sea	bivalves	Mytilus edulis				more than 80% of the diet of eiders consists o at most times of mussels (Nehls & Ketzenberg)
Nehls et al 1997	common eider	Wadden Sea	bivalves	Mytilus edulis	25		60	see Fig 2.
Nystrom et al 1991	common eider	Skagerrak	bivalves	Mya arenaria	9.3	14.3	19.1	
Nystrom et al 1991	common eider	Baltic sea	bivalves	Mytilus edulis	6.6		30	in 1985
Nystrom et al 1991	common eider	Baltic sea	bivalves	Mytilus edulis	4.8		31	in 1986
Nystrom et al 1991	common eider	Skagerrak	bivalves	Mytilus edulis	2.8		34.2	in 1986
Nystrom et al 1991	common eider	Skagerrak	bivalves	Mytilus edulis				in the Stockholm archipelago, eider juveniles selected all sizes of Mytilus available. However, in the Hallo area (fully marine) there was a preference for sizes up to 42mm in length, even although mussels reached a max length of 110.6mm. A similar preference for smaller prey individuals was found when eider juveniles fed on another mussel Mya arenaria mean 14.3mm range 9.3-19.1 in gut vs mean 22.8 and range 12.5-32.3 available.
Oka et al 1999	tufted duck	Japan	bivalves	Corbicula japonica				male tufted ducks have longer bills than females and during our study they ate larger clams than did the females.
Oka et al 1999	tufted duck	Japan	bivalves	Corbicula japonica				tufted ducks in our study tended to select smaller clams on average than those generally available.
Oka et al 1999	tufted duck	Japan	bivalves	Musculista senhousia				The round shape of Corbicula japonica may facilitate prey size selection by tufties. In contrast, no difference was found between male and female tufties in the size of M senhousia eaten. Both male and female tufted ducks select larger mussels including individuals up to almost the maximum size reported. Because of their shell shape (ie slender as opposed to round) mussels are the favoured prey of tufted ducks as they do not need to spend time selectively avoiding unprofitable mussels during their limited underwater foraging time.

Raffaelli et al 1990	common eider	Ythan	bivalves	Mytilus edulis	15		35	
Raffaelli et al 1990	common eider	Ythan	bivalves	Mytilus edulis	10		25	the sizes preferred by eiders
Richman & Lovvorn 2003	spectacled eider	Alaska	bivalves	Nuculana radiata	6	mainly 12-30	36	
Richman & Lovvorn 2003	spectacled eider	Alaska	bivalves					eiders ignored a variety of prey that are eaten elsewhere but were present there in low abundance, and focussed their foraging on the most abundant prey.
Richman & Lovvorn 2003	spectacled eider	Alaska	bivalves					differences in digestibility, in nitrogen, lipid and energy content and in burial depth in the sediment have important effects on the clams' relative foraging value.
Richman & Lovvorn 2003	spectacled eider	Alaska	bivalves					owing to its shallower burial depth, N radiata always have higher foraging value than Macoma calcarea of the same length, despite the higher digestibility and higher nitrogen and energy content of the latter
Richman & Lovvorn 2003	spectacled eider	Alaska	bivalves					relative foraging value depends strongly on the size (age) structure of the different clam populations, which vary with annual and seasonal differences between species in recruitment, growth and mortality
Scheiffarth et al 2001	common eider	Wadden Sea	crustacea	Carcinus maenas				the occurrence of shore crabs in the diet of eiders wintering in the ….might indicate a shortage of suitable mussels and cockles in the area. These findings also stress the fact that birds wintering in the Wadden Sea cannot rely on one single prey species but need to be able to exploit alternative prey (Zwarts et al 1996)
Swennen 1976	common eider	Wadden sea	echinodermata	Asterias rubens				only 0.2% of the diet

Swennen 1976	common eider	Wadden sea	crustacea	Carcinus maenas				crabs comprise 6% of eiders diet in the Wadden Sea. This is more than their part in the Wadden Sea benthos and may point to preference for crabs by eiders
Swennen 1976	common eider	Wadden sea	bivalves	Cerastoderma edule	20		26	cockles comprise c 40% of the diet in the Wadden Sea (in line with their occurrence in the system)
Swennen 1976	common eider	Wadden sea	bivalves	Cerastoderma edule		smaller sizes	49	captive eiders also showed that the birds selected smaller sized cockles although they can swallow much larger (49mm) cockles.
Swennen 1976	common eider	Wadden sea	gastropoda	Littorina littorea				only 1.8% of the diet
Swennen 1976	common eider	Wadden sea	bivalves	Macoma balthica				only 1.1% of the diet
Swennen 1976	common eider	Wadden sea	bivalves	Mytilus edulis	23		25	Mytilus edulis comprises c 40% of the diet in the Wadden Sea (in line with their occurrence in the system)
Swennen 1976	common eider	Wadden sea	bivalves	Mytilus edulis		well below average size		mussels taken by eiders are well below the average size of those present on mussel beds
Van Gils et al 2005b	tufted duck		bivalves	Dreissena polymorpha				For example, preference for the least PROFITABLE (e/h) freshwater mussels by shellfish eating ducks could not be explained by the CM (Draulans 1982, 1984 and de Leeuw 1999). As these ducks ingest their prey whole too, their intake rates are likely to be constrained by rates at which bulky shell material can be processed. Given that shell mass increases more steeply will prey size than does flesh mass (De Leeum 1999), those smallest mussels are of the highest digestive quality (e/k). This seems a likely explanation for what Draulans (1984) has called suboptimal size selection.
Ydenberg & Guillemette 1991	common eider	St Lawrence	bivalves	Mytilus edulis	1		8	

Appendix 10 Notes concerning the instantaneous intake rate and functional responses of diving ducks

source	species	food item	prey size	prey depth (cm)	equation	dependent/ independent variables	min	value	max	comments
Richman & Lovvorn 2003	a type II functional response (limited by handling time)…often typifies diving duck foraging on benthic foods									
Richman & Lovvorn 2003	effects of prey depth have seldom been studied for diving ducks									
Richman & Lovvorn 2003	nutrient and energy content, digestibility and crushing resistance of shells can vary with both species and size of bivalves and various studies have shown size selection of bivalves by diving ducks (none of these are on scoters though, all being of tufted ducks or eiders). In these studies, preference for smaller bivalves than expected was explained by differential availability, handling times, effects of meat: shell ratios on nutrient gain relative to passage rates or as a means to avoiding prey that are too large to swallow. Resistance of shells to crushing in the gizzard may also affect selection of species and sizes of bivalve prey									
Richman & Lovvorn 2003	velvet scoter	Macoma balthica	18-24mm	4	I=0.7483X/(591+X)	I=clams consumed per sec on the bottom and X=clams per sq m	intake rates of smaller clams 18-24mm were limited by clam density up to at least 2000/sq m			
Richman & Lovvorn 2003	velvet scoter	Macoma balthica	24-30mm	4	I=0.496X/(209+X)	I=clams consumed per sec on the bottom and X=clams per sq m	intake rates of larger clams 24-30mm were more limited by handling time at densities >400/sq m			

Richman & Lovvorn 2003	velvet scoter	Macoma balthica	18-24mm	7	I=0.5396X/(682+X)	I=clams consumed per sec on the bottom and X=clams per sq m	intake rates of smaller clams 18-24mm were limited by clam density up to at least 2000/sq m
Richman & Lovvorn 2003	velvet scoter	Macoma balthica	24-30mm	7	I=0.2955X/(139+X)	I=clams consumed per sec on the bottom and X=clams per sq m	derived from the other 3 measured responses
Richman & Lovvorn 2003	velvet scoter	Nuculana radiata					not significantly different to the Macoma FR
Richman & Lovvorn 2003	spectacled eider	Macoma balthica					not significantly different to the Macoma FR of the velvet scoters
Richman & Lovvorn 2004	a type 2 functional response in which IR increases with prey density up to an asymptote where intake is limited by handling time, often typifies diving duck foraging on benthic foods (Takekawa 1987 thesis, Giles 1990, Lovvorn & Gillingham 1996 and Richman & Lovvorn 2003)						
Richman & Lovvorn 2004	scaup (lesser)	Potamogeton pectinatus tubers	<6 and 6-12mm	3	I=3.752X(3260+X)	I=tuber pieces consumed per sec on the bottom and X=tuber pieces per sq m	At depths of both 3cm and 6cm intake rates continued increasing with increasing tuber density up to at least 4000 tubers/sq m

Richman & Lovvorn 2004	scaup (lesser)	Potamogeton pectinatus tubers	< 6mm	6	I=0.657X/(4018+X)	I=tuber pieces consumed per sec on the bottom and X=tuber pieces per sq m	At depths of both 3cm and 6cm intake rates continued increasing with increasing tuber density up to at least 4000 tubers/sq m			
Richman & Lovvorn 2004	scaup (lesser)	Nuculana radiata	<12mm	3	intake rates by two scaup feeding on freshly thawed clams at densities of 100, 250, 500 and 1000 clams/sq m did not differ from those of four scaup feeding on tubers at the same densities. These results indicate that functional responses based on feeding trials with tubers can be extrapolated to freshly thawed clams.					
Lovvorn & Gillingham 1996	canvasback	Vallisneria americana (buds)			our analyses indicate that foraging profitability and amount of viable habitat are most affected by variations in FOOD-ITEM SIZE (MASS PER BUD) AND IN LOCOMOTOR COSTS OF DESCENT AS INFLUENCED BY WATER DEPTH. The gradient and asymptote of the FR (buds eaten per sec v buds per sq m) were much less important probably because unlike our functional responses, the x axis is not truly biomass					
Lovvorn & Gillingham 1996	canvasback	Vallisneria americana (buds)			variations in water temperature above 0 have relatively little effect on foraging costs					
Lovvorn & Gillingham 1996	canvasback	Vallisneria americana (buds)			variations in mass per prey item (bud) alter profitability much more than do variations in bud metabolisable energy, mean bud density or intake rates at different bud densities					
Lovvorn & Gillingham 1996	canvasback	Vallisneria americana (buds)			variations in bud dispersion have relatively minor effects on profitability in this habitat					
Lovvorn & Gillingham 1996	canvasback	Vallisneria americana (buds)								

Lovvorn & Gillingham 1996	canvasback	Vallisneria americana (buds)		2.5 - 6.4	I=0.193X/(29.5+X)	I=buds consumed per second at the bottom and X=number of buds per sq m				fitted to the empirical data of Takekawa's 1987 thesis
Lovvorn & Gillingham 1996	canvasback	Vallisneria americana (buds)								assume canvasbacks search for buried winter buds by touch
Lovvorn 1994	canvasback	Vallisneria americana (buds)			I=0.0727X**0.552	I=tubers eaten PER DIVE and X = tubers per sq m				based on data from Takekawa 1987
Carbone 1995	pochard	mealworms		2.5	I=0.0814+0.0014*X	I=mealworms consumed per second at the bottom, X=mealworms per sq m				both food density and substrate depth influenced the rate of consumption
Carbone 1995	pochard	mealworms		1.25		I=mealworms consumed per second at the bottom	0.67			both food density and substrate depth influenced the rate of consumption
Carbone 1995	pochard	mealworms		3.75		I=mealworms consumed per second at the bottom	0.3			both food density and substrate depth influenced the rate of consumption
Giles 1989	tufted duck(lings)	chironomid larvae			I=-0.51+0.00087*X	I=chironomids consumed per dive, X= chironomid larvae per sq m				range of prey densities from 2000-16,000 per sq m yielded a linear response

Giles 1989	tufted duck(lings)	chironomid larvae	4.4mgdryweight		I=0.6152+0.0003*X	I=chironomids consumed per second on the bottom, X= chironomid larve per sq m	range of prey densities from 2000-16,000 per sq m yielded a linear response. The point of leveling of the curve was not reached in the present study. This is perhaps not surprising since natural chironomid densities can reach at least 4-5 times this value		
Giles 1989	tufted duck(lings)	chironomid larvae	while the food density remained at 2000 per sq m ducklings achieved a feeding success rate of c 1 larvae per dive; this increased to > 2 larvae per dive when the density of chironomids was doubled to 4000 per sq m. The doubling of food density had no obvious effect upon either dive duration or the proportion of dives made on to the food tray						
Systad et al 2000	common eider		ingestion of food per unit time was higher in midwinter than in spring and gizzard size increased to cope with the higher processing rates during the coldest period						
Carbone & Houston 1994	pochard	mealworms			I=0.0814+0.0014*X	I=mealworms consumed per second at the bottom, X=mealworms per sq m			rsq=0.9996 (three density values used (125, 375 and 500 worms per sq m)
Carbone & Houston 1994	pochard	mealworms		1.25		mealworms consumed per sec on the bottom	0.67		rates of consumption (while on the bottom) were significantly affected by sand depth in which mealworms were buried

Carbone & Houston 1994	pochard	mealworms		3.75		mealworms consumed per sec on the bottom	0.3		rates of consumption (while on the bottom) were significantly affected by sand depth in which mealworms were buried
Carbone et al 1996		mealworms	0.087g/ worm						26g live weight of worms = 300 worms
Carbone et al 1996		mealworms	0.087g/ worm						100g live weight of worms = 1150 worms
Lovvorn 1989	canvasback	clams	we lack information on… minimum clam densities required for diving ducks to forage efficiently… More work is needed on clam abundance and its determinants but also on… foraging efficiency of diving ducks.						
Guillemette et al 1996			a reduction in prey availability can affect the profitability of foraging since diving ducks react promptly to changes in prey density						
de Leeuw 1997	tufted ducks	mealworms		2		mealworms consumed per sec (on the bottom)	0.46		consumption rate of mealworms declined significantly as the depth of the sand in which the prey were buried increased
de Leeuw 1997	tufted ducks	mealworms		4		mealworms consumed per sec (on the bottom)	0.14		consumption rate of mealworms declined significantly as the depth of the sand in which the prey were buried increased

de Leeuw 1997	tufted ducks	mealworms	rates of consumption did not affect foraging time (on bottom) in Pochard (Carbone & Houston 1994) nor did intake rate have a strong effect on the predicted foraging time (Houston & Carbone 1992). ie higher or lower IR does NOT affect how long birds spend foraging on the bottom!!!!!!!						
de Leeuw 1997	tufted ducks	mealworms				gFW consumed per sec diving	0.04		maximum intake rate recorded
de Leeuw 1997	tufted ducks	Dreissena	due to the low flesh content of mussels, daily consumption was extremely high (up to 3times the birds body mass of 600g)						
de Leeuw 1997	tufted ducks/ scaup	Dreissena	daily consumption of mussels (on the basis of fresh mass) was about 2-3 times the body mass of the birds because of the large water content and shell content and consequently low nutritional value of the mussels						
de Leeuw 1997	tufted ducks/scaup	Dreissena	scaup proved more efficient foragers at low mussel density than tufted ducks but intake rates seemed unaffected at densities of mussels higher than c 100gFW per sq m						
de Leeuw 1997	scaup	Dreissena				gFW per sec underwater		0.46	at 1m depth
de Leeuw 1997	scaup	Dreissena				gFW per sec underwater		0.42	at 3m depth
de Leeuw 1997	scaup	Dreissena				gFW per sec underwater		0.36	at 5m depth
de Leeuw 1997	scaup	Dreissena	7-30mm		I=0.45X/(7.4+X)	gFW per sec underwater (1.5m deep)	Apparent intake rate while underwater based on timing and counting of dives and before and after measurement of mussel densities etc. The max value of 0.45 was determined from intake rates observed in scaup feeding in diving cages at mussel densities of > 2000 gfw per sq m. The searching coefficient is the only parameter fitted here having forced in the asymptotic value first		

de Leeuw 1997	tufted duck	Dreissena	7-30mm		a type 3 sigmoid curve was fitted but the eqn is not given	gFW per sec underwater (1.5m deep)		0.35	this is the asymptotic value determined as described above for scaup (ie record No 45)
de Leeuw 1997	tufted ducks/ scaup	although the food intake rate itself is usually NOT LIMITING the energy procurement, the efficiency of food gathering may indirectly influence the amount of food to be processed, and thus the time needed for food processing, owing to the high feeding costs in these birds. Diving costs contribute c 25% to the DEE of scaup and tufties in winter, while the energy costs of food processing account for a similar proportion. A decrease in INTAKE RATE results in higher diving costs to obtain a GIVEN QUANTITY of food. This extra diving cost must be compensated by a higher DAILY food intake, which also increases the food processing costs per day and in turn, further increases diving cost to obtain this EXTRA FOOD. Thus, diving ducks face the problem that any adverse effect on feeding performance will disproportionately increase total feeding effort on a daily basis and consequently increases in DEE and foraging times.								
de Leeuw 1997	scaup	Dreissena	7-30mm	Depletion reduces, however, the density of the food source and this will increase the searching effort. From the functional response curves, it appeared that scaup were feeding very efficiently at low mussel densities. This suggests that searching for food is only limiting at EXTREMELY LOW DENSITIES while handling prey is usually limiting.					
de Leeuw 1997	scaup	Dreissena	7-30mm	the result of the patch experiment suggests that scaup prefer to deplete patches SEQUENTIALLY rather than constantly searching for sites with high food densities. This is in accordance with the expectation that handling time mainly determines intake rate and only at very low densities will high searching effort per prey item affect the intake rate. With a flat functional response and a limited perceptive ability the model should indeed predict that birds stay put and deplete patches a lot before moving to another patch.					
de Leeuw 1997	tufted duck	Dreissena	7-30mm	intake rates of tufties were considerably lower at low mussel densities than the intake rates of scaup					

de Leeuw 1997				as a consequence of increasing searching effort with depletion, diving may become too costly for further exploitation of the food source and ducks may have to give up foraging in that patch (BASED ON NET ENERGETIC REWARD RATHER THAN JUST INTAKE RATE)						
de Leeuw 1997	tufted duck	Dreissena		a reduction in foraging success (apparent intake rate per sec underwater) of 20% from the maximum (asymptotic value) will incur an increment in DEE of 25% in tufted duck. Because of these extremely narrow margins we may expect that diving ducks favour areas with high densities of mussels and a high probability of encountering mussels.						
de Leeuw 1997	tufted ducks/ scaup			tufted duck also seem more sensitive to variation in mussel density than scaup probably because searching efficiency is lower (ie a shallower functional response) and a reduction in density more strongly reduces AIR and hence increased DEE						
Lovvorn & Gillingham 1996	canvasbacks			Within generally suitable habitat, water depth and food item size appear more important then food item density per se in limiting sustainable populations of diving ducks (but if one was to have biomass density on the x axis by multiplying bud density by mass per bud, one would probably find biomass density to be even more important)						
Mori & Boyd 2004	fur seal			..indicators of energy intake suggest that the functional response of fur seals feeding on krill is highly non-linear (Boyd and Murray 2001)						
Giles 1989	tufted ducklings			increases in the standing crop of potential food organisms for diving ducks and ducklings can lead to instant improvements in feeding rate						
Lovvorn 1989	canvasbacks			The relation between tuber (food) abundance in core samples and tuber (food) availability to canvasbacks (ducks) is a complex function of food depth (below sediment surface), substrate hardness and disturbance factors, and work is needed to clarify these relationships						
Nehls 1995	common eider	mussels			1.65 mussels/min					head dipping in summer
Nehls 1995	common eider	mussels			1.3 mussels/min					head dipping in autumn

Nehls 1995	common eider	mussels			1.1 mussels/min					head dipping in winter
Nehls 1995	common eider	mussels			1.3 mussels/min					diving in summer
Nehls 1995	common eider	mussels			1.0 mussels/min					diving in winter
Nehls 1995	common eider	mussels	although size selection patterns vary seasonally, the intake rate achieved (mussel flesh per unit time) varies little in relation to time of year and foraging mode employed (head dipping or diving)							
Nehls 1995	common eider	mussels	30-50mm					0.8-0.9g AFDW/min		
Approp Assess 2005	common eider	mussels	we do not have information on what prey density eider require to forage profitably							
Guillemette 1994	common eider	mussels	c 10mm	3.8g shell per minute is the value given for the rate at which eiders ingest shell material. Given the stated value that shells comprise 63.4% of the total mass of mussels of this size, this yields an overall intake rate of fresh mussel mass of 6.00g fresh mass per minute while actively feeding						
Guillemette 1998	common eider	mussels	c 10mm					6.1g whole mussels per min		
Halsey et al 2003	tufted duck	maggots	the ducks may have decreased foraging time in response to the decreased density of maggots over a trial (depletion) which is predicted by the marginal value theorem (in contrast to the possibility that as prey become scarcer diving birds may have to spend more time foraging in order to find the scarcer prey on each dive)							

Hario & Ost 2002	common eider	mussels	3.4-5.6mm	Presents data on total time spent underwater per feeding bout for birds feeding in c 8m water depth. Assuming that birds give up feeding when they have filled their oesophagus (80g fresh mass) then one can work out the intake rate per sec underwater. Using Guillemette's equations one could work out dive durations, travel times, surface times and on-bottom times for dives in 8m depth and then work out the number of dives made and total on bottom time during which this 80g is gathered and thence intake rate per sec on the bottom						
Hario & Ost 2002	common eider	mussels	3.4-5.6mm					4.5g shell material per minute actively feeding (ie within a feeding bout)		(80g * 85.4%shell / 15.2 mins per bout)
Hario & Ost 2002	common eider	mussels	3.4-5.6mm					1.5g shell material per minute actively feeding (ie within a feeding bout)		(80g * 85.4%shell / 45.0 mins per bout)
Hario & Ost 2002	common eider	mussels								collecting the meal is far more laborious for females feeding in an area of low prey density including small prey size
Leopold 2002	common eider	cockles	45.2mm							cockles in the area were very large, but at a density of 0.31 per sq m, eiders could not have been foraging on them profitably.

Rizzolo et al 2005	harlequin duck									..and capture success would likely be reduced by decreased prey density…..
Raffaelli et al 1990	common eider	mussels	15-35mm					0.34 mussels per min		capture rate (per sec spent foraging) for single mussels. Not sure if this should be added to the rate at which clumps captured assuming that birds do both while foraging rather than one or the other)
Raffaelli et al 1990	common eider	mussels	15-35mm					0.75 mussel clumps per min		capture rate (per sec spent foraging) for clumps of mussels. Not sure if this should be added to the rate at which single mussels captured assuming that birds do both while foraging rather than one or the other)

Appendix 11 Notes concerning the assimilation efficiency of diving ducks

source	species	parameter	min	value	max	comment
Guillemette & Larsen 2002	common eider	digestibility		0.85		source is de Leeuw 1997
Nehls 1995	common eider	% ingested energy expended for digestion of mussel flesh (SDA)		14%		Fig 5.12 this figure is consistent with the 85% value we use for assimilation efficiency of mussel flesh. This value is constant irrespective of the length of the mussels involved.
Nehls 1995	common eider	% ingested energy expended for digestion of whole mussels including shells	7%		16%	the relative costs of shell crushing increased from 7% of the ingested energy in a 30mm mussel to 16% in a 50mm mussel. This is not a linear relationship though across the full range from 15mm - 60mm and will in any case vary between lay and natural bed mussels!!!!!
Nehls 1995	common eider	% ingested energy expended on heating the food		10%		as much as 10% of the ingested energy is required to heat the mussels when water temperatures are low.
Nehls 2001	common eider	% assimilated energy spent on crushing mussel shells		20%		
Nehls 2001	common eider	% assimilated energy spent on digesting mussel flesh		20%		
Nehls 2001	common eider	% of assimilated energy spent on heating the food and excreting salt				much less than shell crushing and digestion but still adds to the total cost of food processing
Richman & Lovvorn 2003	common eider	assimilation efficiency when eating Nuculana radiata		0.573		including shells (Nuculana radiata)

Richman & Lovvorn 2003	common eider	assimilation efficiency when eating Macoma calcarea		0.544		including shells (Macoma calcarea)
Richman & Lovvorn 2004	scaup (lesser)	assimilation efficiency		0.505		including shells (Potamocorbula amurensis)
Richman & Lovvorn 2004	scaup (lesser)	assimilation efficiency		0.45		including shells (Macoma balthica)
Richman & Lovvorn 2004	black ducks	assimilation efficiency				Jorde & Owen (1988) found higher digestibility for blue mussels than for soft shelled clams (Mya arenaria) when the ash content of mussels was about 12% lower.
Richman & Lovvorn 2004		assimilation efficiency				variations in digestibility between these and other species may be partly explained by differences in the relative fractions of structural and soluble carbohydrate
Van Gils et al 2005b	red knot	assimilation efficiency		73%		for flesh only (source Piersma 1994)

Appendix 12 Notes concerning the energetics of diving ducks

source	species	parameter	min	value	max	comment
Butler 2000	tufted ducks	energetic cost of diving		3.5 * RMR		when diving to depth of 1.7m for 14.4 secs in a tank. This is the same as the energetic cost of swimming on the surface at their max sustainable speed of 0.78m per s (data from Woakes & Butler 1983)
Criscuolo et al 2000	common eider	costs of salt processing				salt intake leads to an immediate increase in metabolic rate and thus in energy expenditure (Nehls 1996)
Green et al 2005	penguins	cost of diving				shows that there is a decline in resting oxygen consumption rate in winter that facilitates a greater diving performance in winter. This may be caused by changes in the fat distribution and extent of internal insulation such that fatter birds have lower thermoregulatory losses and so lower basal oxygen consumption rates and so can effect better diving performance. A progressive improvement in diving ability due to a reduction in energetic costs has not previously been observed in a mature diving animal. Juvenile diving animals COMMONLY show an improvement in their ability to dive during their development. It seems clear that the decrease in dive cycle oxygen consumption and increase in diving capacity in macaroni penguins are facilitated by this drop in minimum or basal metabolic rate. Seasonal variation in BMR has been demonstrated in many species including seals (various refs).
Green et al 2005	penguins	cost of diving				Other studies have shown that penguins have no thermoneutral zone in water and metabolic rate increases with decreasing water temperature. In little penguins this trend occurs until a critical temperature , beyond which metabolic rate increases sharply (ref)
Green et al 2005	penguins	cost of diving				It is suggested by these authors that a complex interaction between nutritional state, vasoconstriction, fat deposition and fat mobilisation causes a decrease in thermal conductance of around 25% and therefore a substantial reduction in metabolic rate.

Green et al 2005	penguins	cost of diving				This simple model shows us that small increases in insulation (ie better body condition) particularly internal insulation (ie fat) and or water temps can have a large effect on the reduction of metabolic rate (and therefore scope for greater diving performance??) SUGGEST POSSIBILITY OF INCLUDING A BODY MASS DEPENDENT FACTOR TO INFLUENCE THE COST OF DIVING IN THE MODEL SUCH THAT LEANER BIRDS INCUR GREATER COSTS?)
Green et al 2005	penguins	cost of diving				In great cormorants, water temperature, body temperature and body fat thickness were found to be major contributors to diving energetics (Gremillet et al 1998)
Gremillet & Wilson 1999	great cormorant	cost of diving				water temperature and dive depth influenced diving costs drastically. NB both of these factors are included in the scoter/eider model
Gremillet & Wilson 1999	great cormorant	cost of diving				however, the model predicts that cormorant foraging parameters are most strongly influenced by prey availability (strictly the permitted values of catch per unit time (g/min) rather than prey availability per se unless cormorants functional response is entirely linear) so that even limited reduction in prey density (25% reduction in CPUT) makes birds unable to balance energy needs.
Gremillet & Wilson 1999	great cormorant	cost of diving				the model identifies major intersexual differences with respect to sensitivity to water temperature, water depth and prey availability (females much more likely to suffer sooner under adverse circumstances). This is principally due to gender-linked differences in CPUT values used in the model although SEXUAL DIMORPHISM (males are c 40% heavier than females) also plays a role in influencing the surface area/vol ratios of the birds and thus their thermoregulatory costs.
Guillemette 1994	common eider	cost of flight		14 * BMR		using the empirical model of Masman & Klaassen (1987) but having to extrapolate to do so.

Halsey et al 2003	tufted ducks	cost of diving				there was a significant difference between the two curves (cumulative oxygen levels over surface times following dives with and without additional foraging costs (stones on the food tray)) suggesting that the ducks increase the rate of oxygen uptake by their own volition during surface periods in between energetically more costly dives. ie the oxygen gain rate curve is NOT a constant.
Halsey et al 2003	tufted ducks	cost of diving				the ducks are actively increasing the rate of oxygen uptake while on the surface in between energetically more costly dives, perhaps by an increase in respiratory frequency. Because increased tachycardia and respiratory frequency increases surface costs while decreasing recovery time and increasing time at the foraging site, the optimal foraging in air-breathing divers appears to be more complex than has been previously appreciated.
Hawkins et al 2000	common eider	aerobic dive limit			51 secs	based on tufted duck value of 41.5ml O2 per kg and using the mean VO2 value of 49.0mlO2perkgpermin ie 41.5/49 * 60secs
Hilgerloh 1997	common eider	basal metabolic rate				BMR = 3.56 *Weight(kg)**0.734 for non-waders (Aschoff & Pohl 1970)
Jenssen et al 1989	common eider	basal metabolic heat production (W per kg)		3.68		at air temperatures between 32 and 1.5 degrees C
Jenssen et al 1989	common eider	basal metabolic heat production (W per kg)		H = 3.46 - 0.07*airtemp		equation that describes increasing heat production at air temps lower than minus 4.5 degrees
Jenssen et al 1989	common eider	basal metabolic heat production (W per kg)		3.83		at water temperatures between 25 and 16 degrees C
Jenssen et al 1989	common eider	basal metabolic heat production (W per kg)		H = 5.48 - 0.09*watertemp		equation that describes increasing heat production at water temps lower than 15 degrees
Jenssen et al 1989	common eider	Tlc (air)	-4.5		1.5	

Jenssen et al 1989	common eider	Tlc (water)		15		the Tlc in water is higher than in air probably due to the decreased insulative properties of the plumage in water.
Jenssen et al 1989	common eider	body temperature (core)		39.6		in air. This is a low value and may be because the birds were winter acclimatized ie they lower their core body temp in winter to reduce thermoregulatory costs
Jenssen et al 1989	common eider	body temperature (core)		40.4		in water. This is a low value and may be because the birds were winter acclimatized ie they lower their core body temp in winter to reduce thermoregulatory costs
Jenssen et al 1989	common eider	basal metabolic heat production (W per kg)				did not differ between eiders exposed to air or water being 104% and 96% of the predicted values based on Aschoff & Pohl (1970)
Jenssen et al 1989	common eider	thermal conductance				As an adaptation to wintering in cold waters the common eider has evolved a low-thermal conductance. This reduces the energetic costs of wintering. Thus, the nutritional demands are also decreased in a period of the year when the temperatures are low and when the short day length may reduce the time available for feeding
Nehls 2001	common eider	metabolic rate				may double in response to a single meal of a dozen mussels and remain elevated for 2-5 hours due to internal processing of food.
Nehls 2001	common eider	costs of food processing				digestion is an energy consuming process and the same is true for shell crushing and warming the food to body temperature. And the excretion of salt.
Nehls 2001	common eider	cost of shell crushing				increases exponentially with mussel shell length, reflecting that shells get much thicker as mussels grow.
Scheiffarth & Nehls 1997	common eider	basal metabolic rate				BMR = 3.56 *Weight(kg)**0.734 for non-waders (Aschoff & Pohl 1970)

Appendix 13 Notes concerning the duration of dives by diving ducks

source	species	parameter	minimum	value	maximum	comments
Beauchamp et al 1992	common eider	dive duration				should be longest in fruitless dives
Bustnes & Lonne 1997	common eider	dive duration (s)			60	dives of common eiders usually last 30-60 secs (Ydenebrg & Guillemette 1991, Beauchamp et al 1992)
Bustnes & Lonne 1997	king eider	dive duration (s)			>90	wintering king eiders mostly dive for more than 90secs (Systad & Bustnes unpub data)
Cramp & Simons vol 1 1977	velvet scoter	diving behaviour				synchronised diving for food reported
Dunthorn 1971	common eider	dive duration (s)	6		60	the eiders collected the mussels during dives lasting from 6 to 60 seconds
Guillemette et al 2004	common eider	dive duration (s)	8		80	for one of the four females in summer
Guillemette et al 2004	common eider	dive duration (s)			45	for the other three females in summer
Hario & Ost 2002	common eider	dive duration (s)		34.9		at one study site
Hario & Ost 2002	common eider	dive duration (s)		36		at one study site

Hario & Ost 2002	common eider	diving time (total during a dive bout) (mins)	24.7		NB this is the time underwater required to accumulate 80g of fresh mussel mass to fill the oesophagus (assuming that a feeding bout is ended when the oesophagus is full). From this one could work out the intake rate (g fresh mussel mass per sec underwater). However, without knowing or estimating the number of dives per bout this cannot be turned into intake rate per second on the bottom
Hario & Ost 2002	common eider	diving time (total during a dive bout) (mins)	7.2		NB this is the time underwater required to accumulate 80g of fresh mussel mass to fill the oesophagus (assuming that a feeding bout is ended when the oesophagus is full). From this one could work out the intake rate (g fresh mussel mass per sec underwater). However, without knowing or estimating the number of dives per bout this cannot be turned into intake rate per second on the bottom. At this site the total biomass of mussels of the preferred size was fivefold greater than at the other site where total dive time per feeding bout was 24.7mins
Hario & Ost 2002	common eider	feeding bout duration (min)	45		at one study site
Hario & Ost 2002	common eider	feeding bout duration (min)	15.2		at one study site
Hario & Ost 2002	common eider	feeding bout duration (min)	13.2		source Guillemette et al 1992
Hario & Ost 2002	common eider	feeding bout duration (min)	10 to 20		source Ydenberg & Guillemette 1991
Hario & Ost 2002	common eider	feeding bout duration (min)	10 to 20		source Nehls 1995
Hario & Ost 2002	common eider	resting bout duration (min)	7.9		at one study site

Hario & Ost 2002	common eider	resting bout duration (min)		10.9		at one study site
Nehls 1995	common eider	dive duration (s)	1.3	16.8	32	summer Table 5.2 (mean +/- 1.96sd)
Nehls 1995	common eider	dive duration (s)	5	19.4	34	winter Table 5.2 (mean +/- 1.96sd)
Nehls 1995	common eider	diving duration				unsuccessful dives are longer than successful dives (Figure 5.5)
Nehls 1995	common eider	dive duration (s)			45	Figure 3.2
Nehls 1995	common eider	dive duration (s)	5		50	Fig 7.8
Nehls 1995	common eider	diving frequency (dives per hour)			c30	with an exception of one bird on one day, the max value was c 30 dives per hour. The exceptional bird did up to 60 dives per hour Fig 7.11
Nehls 1995	common eider	pause duration (including handling)		25.3		summer Table 5.2 sum of handling time? And pause time
Nehls 1995	common eider	pause duration (including handling)		31.1		winter Table 5.2 sum of handling time? And pause time
Nilsson 1972	common scoter	dive duration (s)	19		46	for depths of 1-8m
Nilsson 1972	velvet scoter	dive duration (s)	20		46	for depths of 1-8m
Ost & Kilpi 1999	common eider	dive duration (s)		25	45	based on a mean of 25secs and an SD of c 10 seconds (non-tending females)
Ost & Kilpi 1999	common eider	dive duration (s)		32	52	based on a mean of 32secs and an SD of c 10 seconds (non-tending females)
Ost & Kilpi 1999	common eider	dive duration (s)		45	65	based on a mean of 45 secs and an SD of c10 secs (large ducklings)

Pedroli 1982	tufted ducks	diving behaviour				diving was an irregular activity stimulated by collective behaviour. When an individual dived, other members of the group rapidly did the same, this sequence being repeated at least ten times. The diving also stopped rapidly.
Raffaelli et al 1990	common eider	dive duration (s)	10		28	this is the range of mean dive duration values for unsuccessful dives (10s) and those in which birds got clumps of mussels (28s). Dives in which single mussels were caught were intermediate (mean 16.5s)
Ydenberg & Guillemette 1991	common eider	dive duration (s)			72	maximum observed

Appendix 14 Notes concerning the constraints on rates of food intake by diving ducks

source	species	parameter	units	min	value	max	comment
Ball 1994	Canvas back	gut capacity	g fresh mass				the total volume of food eaten must be less than or equal to the capacity of the upper digestive tract multiplied by the number of times the upper digestive tract is emptied during the period concerned.
Ball 1994	Canvas back	gut capacity	ml		33		of the upper intestinal tract only
Bourne 1984	scoters	gut capacity	g fresh mass		80		crop and gizzard
Bustnes & Erikstad 1990	black duck	gut processing rate					common mussels pass through the digestive tract of black ducks Anas rubripes in about 30-40 mins
Bustnes 1998	common eider	gut processing rate					Guillemette (1994) found that eiders ingested blue mussels TWICE AS FAST as they were able to digest them, showing the importance of the digestive constraint. The general problem for these birds is thus not to find food (fast enough) but to locate prey with sufficient energy density to fulfill the daily requirement
de Leeuw 1997	Dreissena	constituents					zebra mussels comprise c 56% water, 6% dry flesh mass and 38% shell
de Leeuw 1997	scaup	gut capacity	g fresh mass		35	40	per feeding bout c 35gFW of mussels were ingested. This is close to the 40gfw of mussels found in the oesophagi of 2322 drowned wild scaup. It appears that the esophagus is filled during a feeding bout and mussels are crushed in the gizzard later
de Leeuw 1997	scaup	gut capacity	g fresh mass		55		the amount that can be in the gizzard and intestines (as opposed to the 35g in the esophagus)
de Leeuw 1997	scaup	gut capacity	g fresh mass		90		the amount in the oesophagus, gizzard and intestines combined

de Leeuw 1997	tufted duck/ scaup	gut capacity					the limited capacity to store food in the body and long digestive pauses imply that diving ducks have to spend a large fraction of the day on the feeding grounds
de Leeuw 1997	scaup	gut processing rate	mins		25		the rate of food processing is apparently the factor that limits crude intake rate over a period of several hours
de Leeuw 1997		gut processing rate	mins				the timing of diving activity is structured by the rate of food processing
de Leeuw 1997	scaup	mean increase in fat mass per day (g)	grams		4		
de Leeuw 1997	tufted duck	mean increase in fat mass per day (g)	grams		3		
de Leeuw 1997	scaup	MMEI (kj/day)	kj/day		1435		
de Leeuw 1997	tufted duck	MMEI (kj/day)	kJ/day		1185		
de Leeuw 1997	scaup	MMEI (kj/hr)	kJ/hr		50		from Kirkwood 1983 allometric equation
de Leeuw 1997	tufted duck	MMEI (kj/hr)	kJ/hr		40		from Kirkwood 1983 allometric equation
Goss-Custard notes	Oyster catcher	gut processing rate	mg wet flesh per sec		4.4		source Kersten & Visser 1996 . This equates to 0.66mg AFDM per sec apparently assuming a conversion from fresh mass to AFDM of 0.15 (Kersten & Visser 1996)

Guillemette 1994	common eider	gut capacity	% of corrected total body mass (ie by having first subtracted the mass of food itself)		8-11%	for birds overfeeding in rafts at dusk. This figure relates to the content of oesophagus, gizzard and intestine combined.
Guillemette 1994	common eider	gut capacity	% of corrected total body mass (ie by having first subtracted themass of food itself)	1.10%		mean value for birds shot while flying
Guillemette 1994	common eider	gut capacity	% of corrected total body mass (ie by having first subtracted the mass of food itself)	3.70%		mean value for birds shot while feeding in small flocks
Guillemette 1994	common eider	gut capacity	% of corrected total body mass (ie by having first subtracted the mass of food itself)	6.40%		mean value for birds shot while raft feeding
Guillemette 1994	common eider	gut capacity	% of corrected total body mass (ie by having first subtracted the mass of food itself)		6%	for the esophagus alone
Guillemette 1994	common eider	gut capacity	% of corrected total body mass (ie by having first subtracted the mass of food itself)		3%	for the gizzard alone

Guillemette 1994	common eider	gut capacity	% of corrected total body mass (ie by having first subtracted the mass of food itself)			6%	for the intestine alone
Guillemette 1994	common eider	gut capacity	% of corrected total body mass (ie by having first subtracted the mass of food itself)			15%	the max possible if all gut compartments filled to capacity simultaneously (which was in fact never observed- the max value seen being 11% of corrected body mass). This suggests that eiders stop feeding BEFORE the maximum capacity of their entire gut is attained- perhaps due to impaired flight capabilities once a threshold wing loading is exceeded- enhanced predation risk
Guillemette 1994	common eider	gut capacity	g			150g	the max observed for esophagus and gizzard combined
Guillemette 1994	common eider	gut capacity	g			150g	the max observed for the intestine
Guillemette 1994	common eider	gut capacity	g			210-230g	the max observed gut contents for all parts of the gut combined (<300g given that when the intestine is full, the esophagus and gizzard generally are not and vice versa -see Fig 3 of paper) NB assuming an average over winter body mass of 1850g all in, these value equate to 11-12% of body mass
Guillemette 1994	common eider	gut capacity	g			165	for feeding eiders
Guillemette 1994	common eider	gut capacity	g			229	for over-feeding eiders in rafts
Guillemette 1994	common eider	gut capacity	% of corrected total body mass (ie by having first subtracted the mass of food itself)			6-9%	eiders feeding 'normally' stopped feeding when the food in their gut represented 6-9% of corrected body mass (ie having first deducted food mass)

Guillemette 1994	common eider	gut capacity	% of corrected total body mass (ie by having first subtracted the mass of food itself)			8-11%	eiders feeding in rafts (at dusk) stopped feeding when the food in their gut represented 8-11% of corrected body mass (ie having first deducted food mass)
Guillemette 1994	common eider	gut capacity	g			203	this was the total fresh mass of material in the gut of a single eider that would not take off when scared (possibly too heavy to take off)
Guillemette 1994	common eider	gut processing rate					rates of ingestion of mussel shells is two times higher than the rate of defecation.
Guillemette 1994	common eider	gut processing rate					evidence from two bird shot at the beginning of a feeding bout suggest that esophagus emptying is a necessary condition for the ingestion of another meal
Guillemette 1994	common eider	gut processing rate					because ingestion and digestion are consecutive processes, the slower one will determine the rate at which energy is assimilated.
Guillemette 1994	common eider	gut processing rate	mins		62.5		when feeding on mytilus edulis (n=3) (source Swennen 1976)
Guillemette 1994	common eider	gut processing rate	mins		67.6		when feeding on cerastoderma edule (n=3) (source Swennen 1976)
Guillemette 1994	common eider	gut processing rate	mins		63.4		when feeding on carcinus maenas (n=5) (source Swennen 1976)
Guillemette 1994	common eider	gut processing rate	mins		58		when feeding on crangon crangon (n=2) (source Swennen 1976)
Guillemette 1994	common eider	gut processing rate	mins		63.3		average of all 4 experimental diets (n=13) (source Swennen 1976)

Guillemette 1994	common eider	gut processing rate	g fresh mass per min	3.72		9.64	this refers to the rate at which food is processed thru the gizzard. The variation depends upon whether it is assumed that eiders process food thru their gizzard while feeding as well as while resting or only while resting. (cf estimated value of 6.0g fresh mass ingested per minute as the intake rate of feeding eiders)
Guillemette 1994	common eider	gut processing rate	g fresh mass per min	2.61		3.62	this refers to the rate at which material is defecated. These values are lower than the estimated rates of processing by the gizzard
Guillemette 1994	common eider	gut processing rate					I estimate that the rate at which prey is ingested lies between the lower and upper estimated working capacity of the gizzard so it is not possible to say whether the crushing activity of the gizzard constrains energy assimilation in this species
Guillemette 1994	common eider	gut processing rate					based on the average transit time for food in eiders (63.3mins - Swennen 1976) I estimated that ingestion rate (6.0gfeshmass per min) is about two times faster than the defecation rate ((2.6-3.6 g per min). This is better evidence that the energy assimilation rate of eiders is constrained by the rate of digestion.
Guillemette 1994	common eider	gut processing rate					most models of diet selection assume that animals maximise their rate of ingestion when foraging. If digestion rate is limiting, the rate at which the prey are ingested no longer determines the assimilation of energy. The rate at which food/energy is assimilated or metabolized MAY be constrained by ingestion when food is scarce, and by digestion when food is abundant but of poor quality (Sibly 1981)
Guillemette 1994	common eider	meal size	g (fresh mass including shells)		80		source Guillemette et al 1992

Guillemette 1998	common eider	gut capacity (gizzard)	g fresh mass		20		ingestion rate of shells is approx twice as high as the defecation rate and concluded that energy assimilation is constrained by digestion in this species
Guillemette 1998	common eider	gut processing rate	g fresh mass per min	2.4		6.1	the rate at which the shells are processed in the gizzard. This is the ultimate factor limiting digestion and hence energy assimilation in this species
Guillemette et al 1992	common eider	gut capacity	g fresh mass	64		93	oesophagus only. Corresponds to 3.5%-5% of body mass
Guillemette et al 1992	common eider	gut processing rate	mins				…digestion rate is much slower than the ingestion rate. We suggest that resting after a meal provides time to process a part of the food ingested and to lose mass by defecation and excretion. It follows that resting bouts can be considered as an obligatory part of the foraging behavior of the eider. Together these considerations stress the importance of measuring the intake rate at THE SCALE OF A FORAGING CYCLE OR A DAY IN ORDER TO TAKE INTO ACCOUNT THE HIDDEN HANDLING TIME THAT IS OCCURRING WITHIN THE DIGESTIVE SYSTEM.
Hario & Ost 2002	common eider	gut processing rate					we found that the digestion rate was the major constraint on energy assimilation rates of female common eider in the western gulf of Finland whereas in the central gulf of Finland, the limiting factor was the ingestion rate (based on Swennen's transit time (63.5mins) and a gut (excluding oesophagus) content of 165g total fresh mass of food). The density of blue mussels of suitable size for eiders was significantly lower at the latter site compared to the former and likely was the main cause for the difference

Hario & Ost 2002	common eider	gut processing rate					when ingestion rate falls below the digestion rate, digestion cannot reach its maximum capacity and what is more, the bird is no longer in a positive energy balance during which body reserves accumulate (theoretical framework presented by King 1961)
Lovvorn & Gillingham 1996	Canvas-back	gut capacity	g dry mass		4.65		maximum content of esophagus which limits prey items consumable per foraging bout
Richman & Lovvorn 2003	common eider	gut capacity (gizzard)	grams		20		
Richman & Lovvorn 2003	common eider	meal size	grams		60-100		
Richman & Lovvorn 2004	scaup (lesser)	gut capacity					time required to clear the oesophagus-proventriculus may limit intake rate by scaup over short periods, but intake rate does not seem to be directly constrained by mean retention time
Stempniewicz 1986	common scoter	gut capacity	g fresh mass		9.7+/-6.9		stomach contents (mean +/1sd)
Stempniewicz 1986	velvet scoter	gut capacity	g fresh mass		18.5+/-15.3		stomach contents (mean +/1sd)
Stempniewicz 1986	velvet scoter	gut capacity					the average weight of the contents of adult females was much smaller than that of adult males, and being smaller than males, had a diet that was rather more like that of common scoters (ie fewer fish and more cardium)

Swennen 1976	common eider	gut capacity (g)			143		this was the total mass of shell material in the gut of a single eider with a digestive tract completely filled with cockles. For one swallowed cockle about half the weight is water and slightly less than half is shell (the rest comprising salt and flesh), so one could double this value to get the total fresh mass gut capacity ie c286g fresh mass. NB this paper gives the breakdown between oesophagus 62-64%, gizzard 17-18% and intestine 19-20% of total gut contents.
Swennen 1976	common eider	gut capacity (g)			162		this was the total mass of shell material in the gut of a single eider with a digestive tract completely filled with mussels. NB this paper gives the breakdown between oesophagus 62-64%, gizzard 17-18% and intestine 19-20% of total gut contents.
Swennen 1976	common eider	gut processing rate	mins		63.5		this is the average value across 13 birds in captivity fed on four different diets (range 51-70 mins)
van Gils et al 2005a	red knot	gut processing rate					However, evidence for the significant role of digestive processing rate shaping functional responses and thus foraging decisions is rapidly gaining momentum (numerous refs including Jeschke et al 2002)

van Gils et al 2005a	red knot	gut processing rate					As the digestive constraint acts on the rate at which SHELL MASS can be processed (Van Gils et al 2003a), selecting higher quality prey (ie the amount of metabolisable energy per gram shell mass e/k, indicating a prey's 'softness'), also yields a higher energy intake rate. This leads to gizzard size (ie processing rate) dependent patch use whenever high quality prey is collected at a slower rate (ie lower density) than low quality prey. IN this case, birds with small gizzards (or those where a low gut processing rate acts as a constraint ie GPR<IR) maximize their energy intake rate by feeding in the patch containing the low density of slowly collectable high quality prey. In contrast, birds with large gizzards (or those with a high gut processing rate ie GPR>IR) maximize their energy intake rate in the patch containing the high density (rapidly collected) low quality prey. (see Hirakawa 1995 and Van Gils et al 2005b)
van Gils et al 2005a	red knot	gut processing rate					Patch choice and prey choice depends on the relative magnitudes of GPR and IR. If a bird's GPR < IR achievable everywhere then a bird would do best to feed on the highest quality prey available. If however, GPR>IR everywhere then a bird would do best by trying to fulfil its GPR even if this means feeding at a high rate on low quality prey.

Van Gils et al 2005b	Oyster-catcher	gut processing rate					Note that Knots, unlike oystercatchers (and perhaps eiders) do NOT posses a large proventriculus (glandular stomach) where they store considerable amounts of flesh (about half of the food collected in a single low tide period) which enables oystercatchers to partly postpone digestion to the period of rest during high tide. With such an apparatus, maximising total amount of energy assimilated over a full tidal cycle may require a filled up proventriculus at the end of the low-tide period. Likely this may be accomplished most effectively by rapid prey collection (ie following the CM by minimising h) and NOT by selecting easy to digest prey.
Van Gils et al 2005b	red knot	gut processing rate					the so-called digestive rate model DRM predicts optimal diets that maximise long-term energy intake rate in such digestion-constrained situations (refs)
Van Gils et al 2005b	red knot	gut processing rate					It turns out that the constraining link in the chain of digestive processes is the rate at which shell mass is crushed and processed.
Van Gils et al 2005b	red knot	gut processing rate					each of the three tests supported the DRM and refuted the CM. Short-term ballast (Shell) intake rates in the first experiment were too high for the digestive system to be able to keep up. In this context, the DRM predicts long-term rate maximising foragers to prefer those prey types that yield high ENERGY ASSIMILATION RATES in other words prey types that contain high amounts of flesh relative to their ballast mass. In line with the DRM. preference of the experimental birds reflected digestive QUALITY and NOT PROFITABILITY

Van Gils et al 2005b	red knot	gut processing rate					In the second experiment, in line with the DRM the birds ate virtually all encountered SMALL Macoma while ignoring most large Macoma.
Van Gils et al 2005b	red knot	gut processing rate					Accepting Jeschke et al (2002) conclusion that animals are mostly digestion rather than handling-limited, suggests that the DRM will be a helpful model in a wide range of species, especially those that swallow large amounts of refractory (ballast) material such as herbivores, but also some carnivores. Especially studies on mollusc eating shorebirds or on other avian mollusciviores (eg Beachamp et al 1992) may want to reinterpret their results in the light of the DRM. For example, preference for the least PROFITABLE (e/h) freshwater mussels by shellfish eating ducks could not be explained by the CM (Draulans 1982, 1984 and de Leeuw 1999). As these ducks ingest their prey whole too, their intake rates are likely to be constrained by rates at which bulky shell material can be processed. Given that shell mass increases more steeply will prey size than does flesh mass (De Leeuw 1999), those smallest mussels are of the highest digestive quality (e/k). This seems a likely explanation for what Draulans (1984) has called suboptimal size selection

Appendix 15 Notes concerning the energy density of the prey of diving ducks

source	location	season	species	parameter	value	age/size	comment
Approp Assess 2005			Mytilus edulis	energy density (kcal g dry flesh mass)	4.9		equates to 20.5kJ/gdm (source Ost & Kilpi 1998)
Beauchamp et al 1992			Mytilus edulis	energy density (kj/gram dry mass)	20.51		
Bustnes & Erikstad 1990			Mytilus edulis	energy density (kcal per g dry flesh mass)	4.9		
Cantin et al 1974			Littorina	energy density (kcal g dry flesh mass)	3.4		
Dauvin & Joncourt 1989	English Channel	all year round average	amphipoda	energy density (j per mgAFDW)	21.1		
Dauvin & Joncourt 1989	English Channel	all year round average	bivalvia	energy density (j per mgAFDW)	19.73		
Dauvin & Joncourt 1989	English Channel	all year round average	decapoda	energy density (j per mgAFDW)	20.52		

Dauvin & Joncourt 1989	English Channel	all year round average	gastropoda	energy density (j per mgAFDW)	19.42		
Dauvin & Joncourt 1989	English Channel	all year round average	ophiuroidea	energy density (j per mgAFDW)	19.51		
Dauvin & Joncourt 1989	English Channel	all year round average	polychaeta	energy density (j per mgAFDW)	21.11		
Dauvin & Joncourt 1989	English Channel	all year round average	amphipoda	energy density (j per mgDW)	20.3		
Dauvin & Joncourt 1989	English Channel	all year round average	bivalvia	energy density (j per mgDW)	18.03		individual values available for 120spp including Abra alba, Spisula elliptica and various Tellinas and Venus spp.
Dauvin & Joncourt 1989	English Channel	all year round average	decapoda	energy density (j per mgDW)	19.22		
Dauvin & Joncourt 1989	English Channel	all year round average	gastropoda	energy density (j per mgDW)	17.83		
Dauvin & Joncourt 1989	English Channel	all year round average	ophiuroidea	energy density (j per mgDW)	17.02		
Dauvin & Joncourt 1989	English Channel	all year round average	polychaeta	energy density (j per	18.93		

				mgDW)			
de Leeuw 1997			Dreissena	energy density			in Lake Ijsselmeer mussels from deeper water tend to have lower flesh contents up to 40% less at 5m cf 2m. This may limit the exploitation of deeper located mussels in addition to the greater diving efforts in deeper water
de Leeuw 1997			Dreissena	energy density (kJ per g dry mass of flesh)	22.5		
de Leeuw 1997			Dreissena	energy density (kJ per g FreshWeight)	0.5		
de Leeuw 1997			Dreissena	energy density (kJ per g FreshWeight)	0.6		
de Leeuw 1997			Dreissena	energy density (kj per g live mass)	0.4-0.6		
de Leeuw 1997			diving ducks	energy density of fat stores (kJ/g)	39.3		

Draulans 1982			Mytilus edulis	energy density (kcal g dry flesh mass)	4.5		
Goudie & Ankney 1986			Mytilus edulis	energy density (kj per g live mass incl shell)	1.92		
Goudie & Ankney 1986			amphipoda	energy density (kj per g live mass)	5.9		
Goudie & Ankney 1986			Idotea baltica	energy density (kj per g live mass)	4.39		
Goudie & Ankney 1986			sea urchins	energy density (kj per g live mass)	1.2		
Guillemette et al 1992			Mytilus edulis	energy density (kJ/g wetmass)	0.966		including the shell/test/carapace
Guillemette et al 1992			sea urchins	energy density (kJ/g wetmass)	0.58		including the shell/test/carapace
Guillemette et al 1992			spider crabs	energy density (kJ/g wetmass)	3.163		including the shell/test/carapace

Guillemette & Larsen 2002			Cardium and Spisula	energy density (kj per g wet mass)	1.5		
Hilgerloh 1997			Mytilus edulis	energy density (kJ g AFDW)	20.77		source Jansson & Wulff (1977) and H Asmus (pers comm)
Jorde & Owen 1988			gammarus	energy density (kcal/gdm)	3.52		true metabolisable energy/gram decreased as food intake increased, which indicated differences in the rate or efficiency of digestion (digestion, absorption and passage rates in the alimentary tract of small amounts of food were more efficient than for larger amounts of food ingested)
Jorde & Owen 1988			Littorina	energy density (kcal/gdm)	0.27		ditto
Jorde & Owen 1988			Mytilus edulis	energy density (kcal/gdm)	0.52		ditto
Jorde & Owen 1988			Mya arenaria	energy density (kcal/gdm)	0.22		ditto
Larsen & Guillemette 2000			Mytilus edulis	energy density (kJ g shellFDW)	21.19		source Rumohr et al 1987. there are other values provided here for other taxa but expressed as kJ per gram wet mass
Lovvorn et al 2003	Bering Sea	march	Macoma calcarea	energy density (kJ/gdm)	*	6-12mm	including shells
Lovvorn et al 2003	Bering Sea	march	Macoma calcarea	energy density (kJ/gdm)	4.278	12-18mm	including shells

Lovvorn et al 2003	Bering Sea	march	Macoma calcarea	energy density (kJ/gdm)	5.645	18-24mm	including shells
Lovvorn et al 2003	Bering Sea	march	Macoma calcarea	energy density (kJ/gdm)	6.324	24-30mm	including shells
Lovvorn et al 2003	Bering Sea	march	Nucula belloti	energy density (kJ/gdm)	4.189	6-12mm	including shells
Lovvorn et al 2003	Bering Sea	march	Nucula belloti	energy density (kJ/gdm)	4.55	12-18mm	including shells
Lovvorn et al 2003	Bering Sea	march	Nucula belloti	energy density (kJ/gdm)	*	18-24mm	including shells
Lovvorn et al 2003	Bering Sea	march	Nucula belloti	energy density (kJ/gdm)	*	24-30mm	including shells
Lovvorn et al 2003	Bering Sea	march	Nuculana radiata	energy density (kJ/gdm)	2.663	6-12mm	including shells
Lovvorn et al 2003	Bering Sea	march	Nuculana radiata	energy density (kJ/gdm)	3.508	12-18mm	including shells
Lovvorn et al 2003	Bering Sea	march	Nuculana radiata	energy density (kJ/gdm)	3.475	18-24mm	including shells
Lovvorn et al 2003	Bering Sea	march	Nuculana radiata	energy density (kJ/gdm)	3.418	24-30mm	including shells

Oka et al 1999			shellfish flesh	caloric content			the caloric content of shellfish is contained almost entirely in the flesh (eg the shell of M senhousia contains only 0.04kJ while the flesh contains 0.856kJ per gram wet weight)
Richman & Lovvorn 2003	Canada	august	Macoma calcarea	energy density (kJ/gdm)	17.97		without shells
Richman & Lovvorn 2003	Canada	august	Nucula belloti	energy density (kJ/gdm)	16.83		without shells
Richman & Lovvorn 2003	Canada	august	Nucula minuta	energy density (kJ/gdm)	16.37		without shells
Scheiffarth & Nehls 1997			marine benthic animals	energy density (kJ g AFDW)	22		source Zwarts & Wanink 1993
Van Gils et al 2005b			marine benthic animals	energy density (kJ g AFDW)	22		source Zwarts & Wanink 1993

Appendix 16 Notes concerning the % of time spent feeding by diving ducks

source	species	parameter	min	value	max	comments
Carbone et al 1996	tuftie/ pochard	% time spent foraging (out of dive cycle)				there was a significant decline in % time spent foraging with water depth in both spp.
Christensen 2000	common eider	% time feeding in daylight		62%		by paired females in inshore waters immediately prior to laying (varying from 7.3h to 8.8hrs as the spring progressed)
Christensen 2000	common eider	% time feeding in daylight		74%		by paired females in offshore waters immediately prior to laying (declining from 11.0h to 7.7h as the spring progressed)
Christensen 2000	common eider	% time feeding in daylight		17%		by paired males in inshore waters immediately prior to laying
Christensen 2000	common eider	time feeding in daylight (hours)	7.3		10.6	paired females prior to egg laying. This is a high level of foraging activity that corresponds well with reports of intensive female foraging during the 2-4 weeks prior to nesting (2 refs)
Christensen 2000	common eider	time feeding in daylight (hours)	4.6		6.7	pre-nesting diving females (deduced from Cantin et al1974)
Christensen 2000	common eider	time feeding in daylight (hours)		4.7h		in summer (calculated from Pethon 1967)
Christensen 2000	common eider	time feeding in daylight (hours)		4h		moulting eiders in Greenland (Frimer 1995)
Goudie & Ankney 1986	common scoter	% time feeding (including pauses between dives)		58%		black scoters and common eiders did not differ in the proportion of time spent feeding (but both higher than long-tailed ducks and harlequins)
Guillemette 1998	common eider	% of time spent diving (ie underwater)	15%		24%	the % time spent diving (ie underwater) during the day decreased significantly from mid-winter to spring.
Guillemette 1998	common eider	% of time spent diving (ie underwater)	17%		22%	in Norway cited from Systad 1995 (thesis)

Guillemette 1998	common eider	% time feeding (in daylight)	33%	46%	56%	compensated for shorter days by feeding for 56% of the time in mid winter, 46% in late winter and 33% in spring. NB THIS IS A MIS-INTERPRETATION OF THE DATA BECAUSE THE ABSOLUTE AMOUNT OF TIME SPENT FEEDING PER DAY DID NOT CHANGE AT ALL OVER THE SEASONS. ALL THAT CHANGES IS THE DURATION OF DAYLIGHT USED AS THE DENOMINATOR TO WORK OUT % FEEDING TIME
Guillemette 1998	common eider	time feeding in daylight (hours)				in winter they forage non-stop from one foraging cycle to the next (where a foraging cycle includes inter-dive intervals AND resting bouts after a feeding bout) with only a few roosting bouts breaking this pattern during the day.
Guillemette 1998	common eider	time feeding in daylight (hours)				two strategies are open to diving birds to increase their ingestion rate per hour of daylight. First, is to increase the duration of feeding bouts within a foraging cycle ie spend less time resting/digesting between foraging bouts. Second strategy is to increase the proportional duration of a diving bout (ie time underwater) within a dive cycle (by lengthening time spent underwater per dive OR decreasing time spent on the surface between successive dives). Thus a diving bird should spend relatively more time diving on the bottom compared to the pause made at the surface between dives. NB this ignores the third strategy which is simply to devote more time per day to active foraging ie to spend more time engaged in foraging cycles (including the obligatory rest/digest periods between feeding bouts) and less time roosting/preening etc.

Guillemette 1998	common eider	time feeding in daylight (hours)				"Feeding duration (per 30min obs period) was computed as the sum of the durations of all dive cycles starting with the start of the first dive and ending with the end of the last dive (thus the pause of the last dive cycle was not included in feeding duration). Thus Guillemette's feeding duration (and hence % feeding time figures) includes only that time spent actively engaged in feeding bouts in a sequence of consecutive dive cycle and DOES NOT include time spent resting between successive feeding bouts.
Guillemette 1998	common eider	time feeding in daylight (mins)	295	319	347	there is NO seasonal variation in the absolute amount of time spent feeding with 319 being the average across all seasons. Thus, eiders DO NOT compensate for shorter daylight hours in mid-winter by increasing their feeding effort. Guillemette's interpretation that they do just because the %daylight time spent feeding is higher in mid winter than in spring is plain WRONG
Guillemette 1998	common eider	time underwater in daylight (mins)		137		average across all three seasons (because there is NO seasonal variation in this)
Guillemette 2001	common eider	% time feeding in daylight (including diving and pausing times but NOT resting bouts between diving bouts while actively foraging)		42%		adult female pre breeding
Guillemette 2001	common eider	% time feeding in daylight (including diving and pausing times but NOT resting bouts between diving bouts while actively foraging)		35%		adult female pre migrating

Guillemette 2001	common eider	% time feeding in daylight (including diving and pausing times but NOT resting bouts between diving bouts while actively foraging)		32%		adult male pre breeding
Guillemette 2001	common eider	% time feeding in daylight (including diving and pausing times but NOT resting bouts between diving bouts while actively foraging)		30%		adult male pre migrating
Guillemette 2001	common eider	time underwater in daylight (mins)		169		females in spring (pre-breeding)
Guillemette 2001	common eider	time underwater in daylight (mins)		147		females in spring (pre-migration)
Guillemette 2001	common eider	time underwater in daylight (mins)		111		males in spring (pre-breeding)
Guillemette 2001	common eider	time underwater in daylight (mins)		122		males in spring (pre-migration)
Hilgerloh 1997	common eider	% time feeding in daylight		22.60%		in winter (source Nehls 1995)
Hilgerloh 1997	common eider	% time feeding in daylight		11.60%		in summer (source Nehls 1995)
Kramer 1988		% time at surface				However, diving birds do not fit the expected pattern well. Dewar (1924) and Stonehouse (1967) observations suggest that in fact the % time at the surface actually decreases with diving depth in many species before increasing again near the maximal limit of observed dives.

Laubhan & Metzner 1999	Stellers eider	% time feeding in darkness		37.80%		Varangerfjord Norway (Fox & Mitchell 1997b)
Laubhan & Metzner 1999	common eider	% time feeding in daylight		56%		Newfoundland (Goudie 1984)
Laubhan & Metzner 1999	goldeneye	% time feeding in daylight		86%		southern coast of Sweden (Nilsson 1970)
Laubhan & Metzner 1999	long-tailed duck	% time feeding in daylight		79%		southern coast of Sweden (Nilsson 1970)
Laubhan & Metzner 1999	long-tailed duck	% time feeding in daylight		83%		Newfoundland (Goudie 1984)
Laubhan & Metzner 1999	Stellers eider	% time feeding in daylight		52.30%		Varangerfjord Norway (Fox & Mitchell 1997b)
Laubhan & Metzner 1999	Stellers eider	% time feeding in daylight (including time on surface between dives within feeding bouts)		70.20%		in winter in a lagoon in Alaska
Laubhan & Metzner 1999	Stellers eider	% time feeding in daylight (including time on surface between dives within feeding bouts)		66.40%		in spring in a lagoon in Alaska
Laubhan & Metzner 1999	Stellers eider	% time feeding in daylight (including time on surface between dives within feeding bouts)		80.00%		in winter in a bay in Alaska

Laubhan & Metzner 1999	Stellers eider	% time feeding in daylight (including time on surface between dives within feeding bouts)		51.30%		in spring in a bay in Alaska
Nehls 1995	common eider	% time feeding in daylight	2%		30%	This is the range of values of % activity per tidal cycle (high tide to high tide in DAYLIGHT) across the months Sept to March. The % increases from 2% in Sept to c10% in October, 18% in November, 28% in January, 24% in February and 30% in March. No data for December. Fig 7.7
Nehls 1995	common eider	% time feeding in daylight	7.5%		23%	This is the range of values of % time spent foraging per tidal cycle (13h) in daylight across the months Sept-March. Sept is the lowest value with an increase to 12.5% in Oct, 22.5% in Nov, 13% in Dec, 22% in Jan, 23% in Feb and 19% in March Fig 7.14
Nehls 1995	common eider	% time feeding in daylight			50% of a low tide perod	even at low water in winter when foraging activity was highest, eiders did not spend more than 50% of their time actively foraging.
Nehls 1995	common eider	time spent foraging per 24 hrs		220 mins		winter
Nehls 1995	common eider	time spent foraging per 24 hrs		160 mins		early summer
Raffaelli et al 1990	common eider	time spent feeding (hours)		5.5 hours		eiders forage on the Ythan mussel beds for about 5.5 hours around the time of low tide (although individual birds may only feed for part of this period)
Raffaelli et al 1990	common eider	time spent feeding PER DAY (hours)		4 HOURS		eiders feed on each low tide, EVEN AT NIGHT, with individual birds feeding for about 4 hours each 24 hour period (H Milne pers comm)
Rizzolo et al 2005	harlequin duck	% time feeding in daylight		70%		and % time feeding in daylight in winter is negatively related to temperature and day length (Goudie & Ankney 1986, Fischer & Griffin 2000)

Rodway & Cooke 2001	harlequin duck	% time feeding in daylight				The influx of herring spawn relaxes constraints on foraging time and birds spend less than half as much time foraging during the day when spawn is available than during the months before and after (Rodway unpub data)
Rodway & Cooke 2001	harlequin duck	% time feeding in daylight				In winter (nov-feb) harlequin ducks extended their feeding time by arriving on average c 9-13 mins earlier than at other times of year and departing about one hour later than when herring spawn abundant in early spring. Even so, the actual time spent on the feeding grounds was least in winter (8.5h in Nov-Feb cf 11.2h in March and 13.9h in April). In winter, arrival and departure times were more synchronous suggesting that most birds required the full daylight period to meet their daily energy requirements. Greater variation in arrival and departure times during spring than winter suggests a relaxation of time constraints as day length increased.
Rodway & Cooke 2001	harlequin duck	% time feeding in daylight		16%		of the daylight time spent near the shore was used for feeding ie 16% of 8.5hrs ie 82 mins feeding per day when herring spawn superabundant. Cf very high values for this small species given in other studies.
Swennen 1976	common eider	% time feeding per 24h		51%		this is the % of quarter hour periods per 24h that captive birds were registered to search for food (averaged over January-June during which not much variation in fact)
Systad & Bustnes 2001	Stellers eider	time spent feeding (hours)	4.6h		6.3h	estimated feeding time (in total) was about 35% higher in midwinter than in spring
Systad et al 2000	eiders (common and king)	% time on feeding grounds				birds spent more time in the study area before and after twilight when the days were short than when the days were long
Systad et al 2000	common eider	time spent diving per day (mins)	73	100	144	longer total time underwater in daylight when more hours of daylight

Systad et al 2000	king eider	time spent diving per day (mins)	57	102	161	longer total time underwater in daylight when more hours of daylight
Systad et al 2000	long-tailed duck	time spent diving per day (mins)	148	232	382	longer total time underwater in daylight when more hours of daylight. NB much longer time spent underwater by the smaller long-tailed ducks cf eiders
Systad et al 2000	eiders	% dive time per day				..especially in December and January when feeding was extended into the afternoon darkness
Systad et al 2000	common eider	% time feeding				extended feeding after dark by common eiders also has been observed at blue mussel beds exposed at low tide
Systad et al 2000		% time feeding				compared to most other waterfowl, sea ducks spend substantial amounts of time feeding, probably because of their low quality diets
Systad et al 2000	common eider	proportion time diving (below surface only ie excluding interdive pauses on surface)	0.169		0.257	increased as daylength shortens (0.169 in April and 0.257 in December)
Systad et al 2000	king eider	proportion time diving (below surface only ie excluding interdive pauses on surface)		0.233		did not change significantly with changing daylength (mean c0.233)
Systad et al 2000	long-tailed duck	proportion time diving (below surface only ie excluding interdive pauses on surface)	0.334		0.546	increased as daylength shortens (0.334 in April and 0.546 in November). This (0.53 midwinter) may be close to the max possible rate for the species

Appendix 17 Notes concerning the daily consumption of food by diving ducks

source	species	season	parameter	min	value	max	comments
Approp Assess 2005	common eider		daily consumption g dry shell mass only per day	740		1820	when feeding on 23mm mussels (source Thompson 1985)
Approp Assess 2005	common eider		daily consumption gdm flesh per day		113		source Ost & Kilpi 1998
Approp Assess 2005	common eider		daily consumption gFW per day				other studies of eider indicate that daily feeding rates can vary significantly
Approp Assess 2005	common eider		daily consumption gFW per day		230		when birds feeding on the smallest mussel sizes only ie 5mm (source Ost & Kilpi 1998). Derived from the value of 113gdm flesh per day which therefore means dry mass = 50% of total live mass which is way in excess of the 6-8% value established in Fig 1 for small mussels by Bustnes & Erikstad 1990. Therefore this 230g figure must be wrong!
Approp Assess 2005	common eider		daily consumption gFW per day		900		when birds feeding exclusively on the largest mussel sizes only ie 40-45mm (source Ost & Kilpi 1998). Derived from the value of 113gdm flesh per day which therefore means dry mass = 12.5% of total live mass which is way in excess of the 4% value established in Fig 1 for large mussels by Bustnes & Erikstad 1990. Therefore this 900g figure must be wrong!

Approp Assess 2005	common eider		daily consumption gFW per day				the feeding rate of eiders vary depending on the size of the mussel taken and its meat content/energy value. Greater masses of larger mussels need to be taken because they have proportionately greater shell content.
Approp Assess 2005	common eider		daily consumption gFW per day (whole mussels)	1500		2700	source Ross & Furness 2000 (1500 for small mussels and 2700 for large mussels)
Approp Assess 2005	common eider		daily consumption gFW per day (whole mussels)		1500		when birds feeding exclusively on 9-15mm mussels only (source Bustnes & Erikstad 1990 cited in Ost & Kilpi 1998)
Approp Assess 2005	common eider		daily consumption gFW per day (whole mussels)		2500		when birds feeding exclusively on the largest mussel sizes only ie 41-43mm (source Ost & Kilpi 1998)
Beauchamp et al 1992	common eider		Daily requirement (g dry mass)		130		
Beukema 1993	oystercatcher	winter (Nov-April)	daily requirement (g AFDW per day)		55		based on field data summarised in Hulscher 1982. This figure is higher than the detailed estimates of Kersten & Piersma (1987) of oyks in outdoor cages which amounted to about 35g at T > 10C and increasing to 50g at sub zero temps. The higher activity levels of birds living in the field justify the use of the higher estimates
Beukema 1993	oystercatcher	May-October	daily requirement (g AFDW per day)		40		based on field data summarised in Hulscher 1982. This figure is higher than the detailed estimates of Kersten & Piersma (1987) of oyks in outdoor cages which amounted to about 35g at T > 10C and increasing to 50g at sub zero temps. The higher activity levels of birds living in the field justify the use of the higher estimates

Bourne 1984	scoters		daily intake rate				assume daily ingestion rate of c 20% of total body weight in whole shellfish (shells included) or 30% of body weight in shellfish flesh only per day.
Bourne 1984	surf scoter		daily intake rate		224		whole clams (g) Assuming daily ingestion rate of c 20% of total body weight in whole shellfish (shells included) or 30% of body weight in shellfish flesh only.
Bourne 1984	surf scoter		daily intake rate		672		whole clams (g) Assuming daily ingestion rate of c 60% of total body weight in whole shellfish (shells included).
Bourne 1984	white-winged scoter		daily intake rate		336		whole clams (g) Assuming daily ingestion rate of c 20% of total body weight in whole shellfish (shells included) or 30% of body weight in shellfish flesh only.
Bourne 1984	white-winged scoter		daily intake rate		1008		whole clams (g) Assuming daily ingestion rate of c 60% of total body weight in whole shellfish (shells included).
Bustnes & Erikstad 1990	common eider		Daily requirement (g dry mass)		113		assuming 4.9kcal/g dry flesh mass
Bustnes & Erikstad 1990	common eider		Daily requirement (kcal per day)		555		
Camphuysen et al 2002	common eider	winter	daily requirement (g AFDW per day)		177.8		assuming 3000kJ/day DEE, 75% assimilation efficiency and 22.5kJ/g AFDM of cockles and mussels (Zwarts & Wanink 1993)
Cantin et al 1974	common eider	captive	Daily assimilation (kcal per day)		516		adult (n=2)
Cantin et al 1974	common eider	captive	Daily consumption (kcal per day)		683		adult (n=2)

Cantin et al 1974	common eider	captive	Daily consumption (kcal per day)		520		on Mytilus
Cantin et al 1974	common eider	captive	Daily consumption (kcal per day)		720		on cockles
de Leeuw 1997	scaup		daily consumption gFW per day		2240		
de Leeuw 1997	tufted duck		daily consumption gFW per day		1607		
Goss-Custard notes	common eider		daily consumption g wet flesh per day	813		1125	These values were derived on the basis of the monthly values for daily consumption (g AFDW) assuming a conversion of 6.25*AFDM = FW ie AFDM= 0.16*FW which is wrong probably
Goss-Custard notes	oystercatcher		daily consumption g wet flesh per day		380		This is the maximum daily amount that can be processed and is estimated on the basis of the observed 4.4mg wet flesh per sec processing rate * 60 * 60 * 24 / 1000.
Goss-Custard notes	oystercatcher		daily consumption g wet flesh per day	226		372	min in June and max in February. These are NOT measured values but estimated on the basis of various energetic expenditure equations. There are values for each month showing seasonal variation that could be used for model validation? But NOT if the model uses the same equations to calculate energy expenditure!

Goss-Custard notes	common eider		daily consumption gAFDW per day	130		180	this is for flesh only and the source data is from Nehls 1995 and Nehls et al 1997. There are monthly values showing seasonal variation. These values are probably measured.
Gremillet & Wilson 1999	great cormorant		daily consumption gFW per day				our results confirm that estimates of Daily Food Intake in great cormorants which are generally recorded during a particular season and for a particular location (ie with specific depth and temperature conditions and for a particular prey density) cannot be directly used for calculations concerning energy requirements for birds living elsewhere. A general application derived from a specific study may underestimate or overestimate real food requirements by more than 100% because food requirements depend upon energy expenditure while foraging (depth and temp dependent) and the amount of time spent foraging depends upon prey availability. They are all related much more in aquatic diving species than say in oyks where foraging is not that much more costly than standing around.
Guillemette 1998	common eider		daily consumption g fresh mass per day (whole mussels)		1500		when birds feeding on mussels <25mm only (source Bustnes & erikstad 1990)
Guillemette 1998	common eider		daily consumption g fresh mass per day (whole mussels)		2500		when birds feeding only on mussels c40mm in length (source Bustnes & erikstad 1990)
Guillemette 1998	common eider	winter	daily consumption gFW per day (whole mussels)	1781	1906	2098	1781g in spring, 1906g in mid winter and 2098g in late winter (eating Mytilus edulis)
Guillemette 1998	common eider		daily consumption gFW per day (whole mussels)		1906		mid winter
Guillemette 1998	common eider		daily consumption gFW per day (whole mussels)		2098		late winter

Guillemette 1998	common eider		daily consumption gFW per day (whole mussels)		1781		spring
Guillemette et al 1996	common eider		Daily consumption (g fresh weight per day (poss incl shells)		2000		on Mytilus
Guillemette et al 1996	common eider		Daily consumption (g fresh weight per day (poss incl shells)		1990		on sea urchins
Hamilton 2000	common eider		daily consumption g dry tissue biomass per day		130		assuming an eider feeding exclusively on mussels eats 130g dry tissue biomass of mussels per day (a mean of estimates from Bedard et al 1980, Bustnes & Erikstad 1990, Egerrup & Laursen 1992 and Hilgerloh 1997)
Hario & Ost 2002	common eider		daily consumption of inorganic matter ie shells (g)	500		2500	various references
Hilgerloh 1997	common eider	winter	daily consumption gAFDW per day		187		source Nehls 1995
Hilgerloh 1997	common eider	summer	daily consumption gAFDW per day		130		source Nehls 1995
Hilgerloh 1997	common eider		daily consumption gAFDW per day				gAFDWconsumedperday = (347.8270*%dayspentfeeding) / (%dayspentfeeding + 19.4369) this function was used to calculate the average daily consumption for each month
Hilgerloh 1997	common eider		daily consumption gAFDW per day	92		183	varying between months
Nehls 1989	common eider	captive birds	daily requirement (g AFDW per day)		138		equivalent to 2.5kg molluscs wet weight, including shells (Swennen 1976). Field studies indicate that this value is in the order of magnitude for wintering eiders

Nehls et al 1997	common eider		daily requirement (g AFDW per day)	130		180	the food demand of eiders changes seasonally increasing from 130 in summer to 180 in winter (Nehls 1995)
Swennen 1976	common eider		Daily consumption (kcal per day)		750		
Swennen 1976	common eider		daily consumption gAFDW per day		107		for captive birds. Range of values = 78g - 151g. Assume an extra 30% for free-living birds to give a mean value of 138g AFDW per day

Appendix 18 Notes concerning the daily energy expenditure of diving ducks

source	species	parameter	value	comment
Approp assess 2005	common eider	daily energy requirement	555kcal	equates to 2322kJ. (Source Ost & Kilpi 1998)
Camphuysen et al 2002	common eider	Daily Energy Expenditure (DEE)	3000kJ	ie 4.3 * BMR source Nehls 1995
de Leeuw 1997	common eider	DEE	4.3*BMR	
de Leeuw 1997	common eider	DEE	4.3*BMR	in winter
de Leeuw 1997	diving ducks	DEE		because of the high energetic costs of getting benthic food underwater and the need to heat large quantities of cold prey, food intake rates have a direct implication for energy and time budgets of diving ducks in addition to habitat parameters. Properties of the prey are supposed to be the primary determinants of food intake rates in this study. For example, handling of mussels may depend on prey size and byssal attachment, while searching for mussels depends on the distribution of the prey (density and patchiness). These prey properties in turn depend on properties of the habitat, IN PARTICULAR WATER DEPTH. WATER DEPTH MAY ALSO AFFECT THE ENERGETIC CONTENT OF THE PREY TOO.
de Leeuw 1997	diving ducks	DEE		foraging costs mainly determine DEE

de Leeuw 1997	scaup	DEE	1063kJ	
de Leeuw 1997	tufted duck	DEE	4.2*BMR	this is close to the upper ceiling of metabolisable energy which can be achieved according to Kirkwood (1983)
de Leeuw 1997	tufted duck	DEE	4.2*BMR	in winter. Costs for thermoregulation and heating up the ingested mussels primarily explained the high DEE in winter. These high costs are probably due to the high costs of feeding on mussels with a low energy density
de Leeuw 1997	tufted duck/ scaup	DEE		minimising DEE at ENERGY BALANCE is here used a currency for habitat selection decisions. DEE is calculated in two steps. First, the daily costs for maintenance and flight are assessed for a certain feeding site and roost (fixed costs) and subsequently, the additive costs are calculated in order to achieve energy balance. For every unit of foraging effort (second spent underwater) energy is gained by food intake (depending on apparent intake rate and energy content of mussels) while the energy costs of diving (per sec) and food processing increase. The energy expenditure at the point where expenses meet the gains equals the DEE at energy balance.
de Leeuw 1997	tufted duck/ scaup	DEE		the increased diving effort with greater water depth has only a moderate effect on DEE when mussel condition is constant with respect to water depth. It is the decline in mussel condition with increasing water depth that leads to the marked increase in DEE with water depth in the Ijsselmeer.
Guillemette 1998	common eider	DEE		energy budgets of small flock eiders were computed for midwinter, late winter and spring (Guillemette unpubl data) (using thermoregulatory data of Jenssen et al 1989 and activity costs of ducks) and were found to be constant. i.e. no seasonal variation in DEE
Hilgerloh 1997	common eider	DEE		assumed to be 3 times BMR in the model of Hilgerloh 1997
Lovvorn & Gillingham 1996	canvasback	DEE	1120kJ	Field Metabolic Rate based on Nagy 1987 allometric equation
Nehls 1995	common eider	Basal Metabolic Rate	700kJ/day	Table 7.4

Nehls 1995	common eider	cost of processing food		The energy expenditure of eiders increases when they ingest food (Fig 5.8) and the more they consume, the greater is the increase in EE above resting levels (Fig 5.10)
Nehls 1995	common eider	cost of processing food		The larger the size of whole mussels consumed, the greater is the increase in EE for digestion above resting levels (Fig 5.11). Fig 5.12 indicates that 15% of the energy ingested in the form of flesh is expended in digestion ie this is the 85% assimilation efficiency figure we use. However, for ingesting mussels whole, the % of energy ingested that is expended in digestion is higher (c20% for 15-20mm mussels and 33% for 60mm mussels). Thus for whole mussels assimilation efficiency will be between 67% and 80% depending upon length (and probably shell thickness too!)
Nehls 1995	common eider	cost of processing food		At high ambient temps 10 degrees C, c 30% of ingested energy is expended in digestion for 43mm whole mussels (cf 15% for the equivalent amount of flesh only). However, at very low ambient temps (below -10 degrees C) this proportion drops to a min of 10% at -25degrees for whole mussels and 5% for mussel flesh (heat substitution?) Fig 5.13
Nehls 1995	common eider	cost of processing food		For the winter months it is assumed (Fig 5.15) that SDA and shell crushing energy costs substitute for thermoregulation by 50% ie that they only incur half the costs and that eiders have to heat mussels to 40 degrees. The assimilation efficiency was assumed to be 75%. IN THE SCOTER MODEL I INCORPORATED THESE COSTS BY REDUCING THE ASSIMILATION EFFICIENCY ACHIEVED.
Nehls 1995	common eider	DEE	3022kJ	This is the winter value. It is made up of BMR (700kJ/day (23%), food gathering by diving and dibbling (7%), shell crushing (17.5%), digestion costs (SDA) (19%), food heating (12.5%), thermoregulatory costs (13%) and an excess for other activities (7%). Table 7.4. It equates to about 4.3*BMR
Nehls 1995	common eider	DEE		eiders energy budget in winter can only be well balanced if heat production from digestion is utilised for thermoregulation. Data indicate that eiders stretch their foraging activity in winter to optimise heat utilisation.

Nehls 1995	common eider	DEE		The tight energy budget of eiders stresses the importance of mussel quality (shell thickness and flesh content) as a criterion for foraging site and food selection.
Nehls 1995	common eider	thermoregulatory costs		The energy expenditure of captive eiders increases with decreasing ambient temps below a lower threshold of c-5 degrees C. The RMR in the thermoneutral zone is c3.75w/kg and this increases to 5.5W/kg at -25 degrees C ie over a temp change of 20 degrees. Fig 5.9

Appendix 19 Notes concerning the body masses of common eiders

source	location	season	months	parameter	min	value	max	age	sex	comment
Cabanac 2003				body condition						several studies have shown that eiders, like other birds and mammals, use both fat and protein reserves as endogenous sources of energy (3 refs). Milne (1976) data on fasting breeding females shows at least two of the phases of mass decline (phases 2 and 3)
Cabanac 2003				body condition						the maximum utilization of endogenous energy was shown to be 95% of the lipid within the body both in winter and breeding period. The maximal utilisaton of protein in these periods was 37% and 52% respectively.
Cabanac 2003		winter		fat stores(g) ie total body fat content						lipid = -168.7 + 0.165 * body mass. So, body fat = 0 at a fat depletion mass of 1022g
Cabanac 2003		winter		protein stores(g) ie total body protein content						protein = 49.4 + 0.142 * body mass
Cabanac 2003	Gulf of St Lawrence	winter		weight (g)		1815			both combined	n = 131 birds (source Cabanac & Guillemette unpub data)

Cabanac 2003		winter		weight (starvation) (g)						In conditions of extreme food shortage a fasting eider may totally deplete its metabolic reserves. Warnes (1988) reported that some starving eiders lost 35-39% of their weight during the winter. Also kervella & Guillemette (unpub) measured a 21-25% weight loss in starving eiders in winter.
Camphuysen et al 2002	Denmark	winter		weight (g)		1770		juv	female	normal masses in Denmark in winter (Cramp & Simmons 1977)
Camphuysen et al 2002	Denmark	winter		weight (g)		2142		adult	female	normal masses in Denmark in winter (Cramp & Simmons 1977)
Camphuysen et al 2002	Denmark	winter		weight (g)		2080		juv	male	normal masses in Denmark in winter (Cramp & Simmons 1977)
Camphuysen et al 2002	Denmark	winter		weight (g)		2251		imm	male	normal masses in Denmark in winter (Cramp & Simmons 1977)
Camphuysen et al 2002	Denmark	winter		weight (g)		2315		adult	male	normal masses in Denmark in winter (Cramp & Simmons 1977)
Camphuysen et al 2002	Baltic	winter		weight (g)		2133		juv	female	wintering eiders in good condition drowned in Baltic (Berndt et al 1993)
Camphuysen et al 2002	Baltic	winter		weight (g)		2588		adult	female	wintering eiders in good condition drowned in Baltic (Berndt et al 1993)
Camphuysen et al 2002	Baltic	winter		weight (g)		2379		juv	male	wintering eiders in good condition drowned in Baltic (Berndt et al 1993)
Camphuysen et al 2002	Baltic	winter		weight (g)		2541		imm	male	wintering eiders in good condition drowned in Baltic (Berndt et al 1993)
Camphuysen et al 2002	Baltic	winter		weight (g)		2816		adult	male	wintering eiders in good condition drowned in Baltic (Berndt et al 1993)
Camphuysen et al 2002	Wadden Sea	winter	Dec-March	weight (starvation) (g)	1160	1384	1500		female	n=8 found freshly dead in Wadden Sea winter 1999-2000

Camphuysen et al 2002	Wadden Sea	winter	Dec-March	weight (starvation) (g)	895	1287	1800	juv	female	n=61 found freshly dead in Wadden Sea winter 1999-2000
Camphuysen et al 2002	Wadden Sea	winter	Dec-March	weight (starvation) (g)	1225	1421	1535	adult	female	n=7 found freshly dead in Wadden Sea winter 1999-2000
Camphuysen et al 2002	Wadden Sea	winter	Dec-March	weight (starvation) (g)	995	1408	1820	juv	male	n=57 found freshly dead in Wadden Sea winter 1999-2000
Camphuysen et al 2002	Wadden Sea	winter	Dec-March	weight (starvation) (g)	1280	1463	1540	imm	male	n=4 found freshly dead in Wadden Sea winter 1999-2000
Camphuysen et al 2002	Wadden Sea	winter	Dec-March	weight (starvation) (g)	1285	1531	1795	adult	male	n=20 found freshly dead in Wadden Sea winter 1999-2000
Camphuysen et al 2002	Wadden Sea	winter	Dec-March	weight (starvation) (g)						the body mass of the dead eiders was 30-45% lower than published data for healthy birds of this subspecies
Guillemette 2001	scotland			fat stores(g) ie total body fat content		160-180		adult	male	more or less constant winter-spring (source Gorman & Milne 1971)
Guillemette 2001	St Lawrence	spring-summer		weight (g)	1900		2600	adult	female	pre-laying
Guillemette 2001	St Lawrence			weight (g)				adult	female	in contrast, the body masses of females upon departure for spring migration are only slightly higher than winter levels (by about 125g Guillemette et al 1992) suggesting that pre-migratory fattening is small in this species (because of high wing-loading problems)
Guillemette 2001	St Lawrence	winter-spring	january-april	weight (g)		1955-1965		adult	male	average value which is constant January to April ie no seasonal change mid-winter to spring

Guillemette 2001	St Lawrence	spring	april	weight (g)		1816		adult	female	only 6-9% higher than their winter levels
Guillemette 2001								adult	male	Gorman & Milne (1971) showed that fat and protein reserves of individual male eiders caught in winter and before the nesting season were almost constant
Guillemette et al 2004		spring		weight (g)		2637		adult	female	when preparing for reproduction in spring
Guillemette et al 2004		winter		weight (g)		1850		adult	female	source Guillemette & Ouellet 2005
Guillemette et al 2004		summer		weight (g)		1400		adult	female	at hatching
Larsen & Guillemette 2000	Kattegat	winter		weight (g)		2300				based on weights of common eiders wintering in the Kattegat (Laursen unpub data)
Milne 1976	Ythan	autumn	august	fat stores(g) ie total body fat content		100		adult	female	
Milne 1976	Ythan	winter	october-march	fat stores(g) ie total body fat content		150		adult	female	
Milne 1976	Ythan	spring	april	fat stores(g) ie total body fat content		400		adult	female	
Milne 1976	Ythan	autumn	august	fat stores(g) ie total body fat content		120		adult	male	
Milne 1976	Ythan	winter	october-march	fat stores(g) ie total body fat content		175		adult	male	

Milne 1976	Ythan	spring	april	fat stores(g) ie total body fat content		175		adult	male	
Milne 1976	Ythan		june	fat-free mass (g)		1150		adult	female	fat free mass at end of incubation
Milne 1976	Ythan	autumn	august	weight (g)		1950		adult	female	
Milne 1976	Ythan	winter	october-march	weight (g)		2050		adult	female	no significant differences could be detected between mean body weights in the months October - March in most years ie overwinter weights are constant
Milne 1976	Ythan	spring	april	weight (g)		2500		adult	female	the pre-breeding increase in body weight of adult females was largely due to deposits of fat accumulated during April ie not earlier in the winter. However, the pre-breeding increase in total fresh mass of females was associated with a corresponding increase in dry weight resulting from increases in both fat and protein.
Milne 1976	Ythan	autumn	august	weight (g)		2190		adult	male	
Milne 1976	Ythan	winter	october-march	weight (g)		2360		adult	male	no significant differences could be detected between mean body weights in the months October - March in most years ie overwinter weights are constant
Milne 1976	Ythan	spring	april	weight (g)		2225		adult	male	
Milne 1976	Ythan	all year		weight (g)				adult		there appears to be no relationship however between overwintering weights and the subsequent mean body weights recorded at other times of the year (ie pre-breeding etc).

Milne 1976	Ythan	winter		weight (g)				juv		a highly significant INVERSE relationship between wintering numbers of eiders and mean overwinter adult body weight can be demonstrated. The data support some homeostatic density-dependent mechanism is operating within the winter population.
Milne 1976	Ythan	winter		weight (g)				juv		Mean weights of first winter birds were lower following good breeding years than after poor breeding years The inverse relationship between mean body weights of 1st winter birds and the number of young fledged each year is statistically significant for both sexes. This might suggest some direct relationship between available food supplies and body weights. If this is so, then one might postulate that the longer term fluctuations in overwintering weights of adults also reflect their available food supplies.
Milne 1976	Ythan	winter		weight (g)		2006		juv	male	after a poor breeding year
Milne 1976	Ythan	winter		weight (g)		1834		juv	female	after a poor breeding year
Milne 1976	Ythan	winter		weight (g)		1809		juv	male	after a good breeding year
Milne 1976	Ythan	winter		weight (g)		1678		juv	female	after a good breeding year
Nehls 1995	Wadden Sea		septemb er	weight (g)		2260		adult	male	Fig 4.7
Nehls 1995	Wadden Sea		october	weight (g)		2350		adult	male	Fig 4.7
Nehls 1995	Wadden Sea		january	weight (g)		2400		adult	male	Fig 4.7
Nehls 1995	Wadden Sea		february	weight (g)		2260		adult	male	Fig 4.7
Nehls 1995	Wadden Sea		septemb er	weight (g)		2060		adult	female	Fig 4.7

Nehls 1995	Wadden Sea		october	weight (g)		2130		adult	female	Fig 4.7
Nehls 1995	Wadden Sea		january	weight (g)		2180		adult	female	Fig 4.7
Nehls 1995	Wadden Sea		february	weight (g)		2060		adult	female	Fig 4.7
Nehls 1995	Wadden Sea		septemb er	weight (g)		2200		juv	male	Fig 4.7
Nehls 1995	Wadden Sea		january	weight (g)		2260		juv	male	Fig 4.7
Nehls 1995	Wadden Sea		february	weight (g)		2170		juv	male	Fig 4.7
Nehls 1995	Wadden Sea		january	weight (g)		2125		juv	female	Fig 4.7
Nehls 1995	Wadden Sea		february	weight (g)		2000		juv	female	Fig 4.7
Nystrom et al 1991	Stockholm	winter	sept-october	weight (g)	1100	1790	2600	juv		n = 35
Suter & Van Eerden 1992		winter		weight (starvation) (g)						Wranes (1988) reports a mass loss of 35-39% in starved eiders in winter.
Swennen 1976	captive	all year	various months	weight (g)	2050	2286	2610	adult	male	n =121
Swennen 1976	captive	all year	various months	weight (g)	1820	2114	2400	adult	female	n=46

Appendix 20 Notes concerning the mortality of diving ducks

source	species	parameter	min	value	max	comments
Approp Assess 2005	common eider	mortality (overwinter) proportion				the loss of access to a substantial feeding area on the lays in The Wash is likely to result in an adverse affect on the eider given that wild mussel and cockle stocks are insufficient to maintain minimum mortality levels in the eider population
Camphuysen 2001	common eider	mortality				In the DUTCH Wadden Sea In December most birds found were identified as juveniles or unaged birds in female plumage (probably also mainly juveniles). The proportion of adult males found dead increased gradually through January-March and markedly in April ie young birds died first.
Coulson 1984	common eider	annual survival	0.756	0.895	1	
Dekker 2001	common eider	mortality				During the mass mortality event relatively big numbers of eiders were concentrated along the shores of the Wadden Sea feeding upon shore crabs which is supposed to be a less preferred prey
Fleet 2001	common eider	mortality				As the Wadden Sea population normally has a higher ratio of males, it appears that proportionally, more females than males died (62% of the 900 birds that were sexed according to plumage characteristics were classed as females (NB maybe they were predominantly juveniles though-see Camphuysen 2001)) in the GERMAN Wadden Sea in winter 1999/2000.
Fleet 2001	common eider	mortality (overwinter) proportion		0.06		…this represents 6% of the total winter population in the region of the German Wadden Sea in 1999/2000
Flint et al 2000	steller's eiders	annual survival		0.899		for females. The lower survival of males compared to females is unusual for waterfowl.
Flint et al 2000	steller's eiders	annual survival		0.765		for males. A shortage of drakes may prevent all females from pairing and reduced breeding propensity may be limiting the reproductive potential of the Steller's eider population

Flint et al 2000	steller's eiders	annual survival		0.946		females 1975-1981
Flint et al 2000	steller's eiders	annual survival		0.827		females 1991-1997
Flint et al 2000	steller's eiders	annual survival		0.874		males 1975-1981
Flint et al 2000	steller's eiders	annual survival		0.761		males 1991-1997
Flint et al 2000	steller's eiders	annual survival				our estimates of annual survival rates for adult female Steller's eiders are similar to common eiders (Reed 1975, Wakeley & Mendall 1976, Coulson 1984) but higher than spectacled eiders
Fox et al 2003	common scoter	annual survival	0.623	0.749	0.843	first year after ringing
Fox et al 2003	common scoter	annual survival	0.715	0.783	0.839	following years. This is higher than Tufted duck and Pochard (0.72 and 0.65) but less than for eiders (0.90)
Fox et al 2003	common scoter	annual survival		0.77		source (Boyd 1962)
Garthe & Huppop 2004	common scoter	annual survival		0.773		source: Krementz, Barker & Nichols 1997
Guillemette et al 1992	common eider	mortality				body mass (and reserves) in ducks in winter is positively correlated with the probability of survival. We have no difficulty imagining that starvation could be a major cause of natural mortality in wintering eiders. sources : Haramis et al 1986, Hepp et al 1986
Kirby et al 1993	scoter spp.	mortality				Unfortunately there is very little hard data on any aspects of the population ecology in seaducks. Relatively little is known about…winter mortality rates.
Krementz et al 1996	common eider	annual survival				despite these concerns, one of the most important life history parameters - annual survival- has yet to be estimated with modern methods for eiders in north America

Krementz et al 1996	common eider	annual survival (females)		0.81		from Wakeley & Mendall 1976. (derived from composite-dynamic life table method which has inherent flaws)
Krementz et al 1996	common eider	annual survival (females)		0.826		from Reed 1975. (derived from composite-dynamic life table method which has inherent flaws)
Krementz et al 1996	common eider	annual survival (females)		0.873		95% CI = 0.8424 - 0.9037. for females only
Krementz et al 1996	common eider	annual survival (females)	0.756	0.895	1	from Coulson 1984
Krementz et al 1996	white-winged scoter	annual survival (females)	0.2	0.773	1.398	se 0.0176. The big range between min and max reflects variation in estimates for individual years based on only a total of 442 adult females. Nonetheless, this is the largest and most complete dataset available for north American scoters. Survival rates of w-w scoters appear to be RELATIVELY HIGH COMPARED TO OTHER NORTH AMERICAN WATERFOWL. (NB this population is hunted but maybe not as heavily as other north American waterfowl spp). Whether survival rates would be even higher in the absence of hunting, as appears to be the case for common eiders (Coulson 1984) is open to conjecture.
Piersma & Camphuysen 2001	common eider	mortality (overwinter) proportion		0.15		between Nov 1999 and June 2000 at least 21,000 eiders died representing an unprecedented 15% of the national wintering population in the Dutch Wadden Sea
Richman & Lovvorn 2003	spectacled eider	mortality				up to 46% of the annual mortality of adult females appears to occur in the non-breeding period when the eiders are at sea. Regardless of the mechanism, modelling indicates that a major limitation on the population is adult mortality much of which occurs away from the breeding area. Source Flint et al 2000
Ross 1983	common scoter	mortality		0.65-0.70		assumption: an overwintering mortality range for subadults of 65-70% cf Bellrose 1978
Suter & Van Eeerden 1992	common eider	mortality				Wranes (1988) and Morner (1982) report some 14000 eider having starved to death in the Skagerak area in the winter of 1981/82 due to a combination of food shortage and low ambient temperatures

Suter & Van Eeerden 1992	scaup	mortality				more female scaup died than males (of starvation during a late winter cold spell in the Wadden sea in 1985/1986)
Swennen et al 1979	common eider	mortality				it is conceivable that female ducklings are generally less resistant to disease and or have a lowered vitality (based simply on a disparity between the sexes in one out of three years) (refers to ducklings in captivity)
Swennen et al 1979	common eider	mortality				combining published data on numbers and sex ratios per area, the figures seem to indicate a slight dominance of males in the total Baltic-Wadden Sea population. Our study has shown that an unbalanced sex ratio can already be established in ducklings in which females have a higher mortality rate. Also in later stages of life females seem to be more susceptible to calamities and epidemics. In the Dutch Wadden sea more adult females than males fell victim to an acanthocephalan parasite (ref). BUT no evidence in this paper for a higher mortality rate amongst adult females when compared to males.